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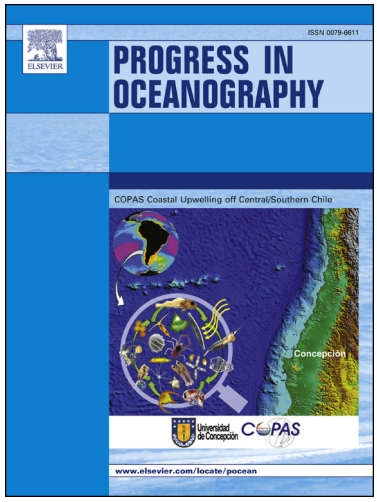

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Mesozooplankton in the Southern Ocean: spatial and temporal patterns from *Discovery Investigations*

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Running head: Mesozooplankton from *Discovery Investigations*

ABSTRACT

Mesozooplankton samples taken during the *Discovery Investigations* in the Southern Ocean in the 1930's were analysed from a series of 5 transects along 80°W. The samples provide a unique level of depth-discrete resolution across large spatial scales, over most of the productive austral season. Stratified net hauls were taken between 0 and 1000 m within the period December 1933 to November 1934. Within the epipelagic (0-100 m), median zooplankton abundance (278 ind. m^{-3}) was ~ 22 times greater than at 1000 m. A 3-4 fold variability of abundance in the epipelagic contrasted with depths > 250 m where variability was <1 fold. Depth was the strongest factor separating samples (ANOSIM, R =0.66 p=0.1%), with a clear biological distinction between epipelagic and upper and lower mesopelagic horizons. Results from multi-dimensional scaling indicated that, when plankton abundance was integrated over all depth horizons, 3 different groups could be identified. These 'communities' were consistent with the spatial extents of Antarctic, Polar Frontal Zone, and sub-Antarctic water-mass regimes. Such groupings became less distinct when considering only deeper horizons (500-1000 m) and excluding seasonal migrants. Seasonal signals across all data became less distinct with depth. Rarefaction analysis indicated that diversity increased with depth. Although depth alone was the most important influence on sample diversity, (r^2= 0.60), water mass regime and month improved the fit (r^2=0.71). Overall plankton diversity was highest in the sub-Antarctic zone. Following atmospheric and ocean warming that has taken place close to the study area in the last 80 years we hypothesise that species richness may increase in the Antarctic water masses as sub-Antarctic species increasingly encroach south.

1. Introduction

Within the world's oceans far more is known about the plankton occupying the epipelagic than the deeper horizons. This is particularly true of the Southern Ocean where the vast majority of investigations have taken place within the surface 200 m. Fewer studies have taken into account the deeper water column and have largely emphasised taxonomy (e.g. Park, 1978, 1983, 1993, Bradford-Grieve, 1994, 1999), or have focused on descriptions of planktonic life cycles and vertical distribution (Andrews, 1966; Voronina, 1972; Atkinson, 1991, Marrari et al., 2011; Wiebe et al., 2011).

Fundamental knowledge of the distribution of plankton abundance and biomass within the Southern Ocean has largely come from the *Discovery Investigations* carried out during the early to middle part of the 20th century. Plankton samples taken with the N70V net have variously been used for regional comparisons of standing stock in the Southern Ocean (Foxton 1956), understanding the circulation of macroplankton (Mackintosh, 1937), elucidating life cycles and distribution of copepods (Andrews, 1966; Ommaney, 1936; Atkinson, 1991) as well as chaetognaths (David, 1955, 1958). Foxton (1956) used over 2,100 stratified N70V net samples (0-1000 m), from 366 *Discovery* stations within the Southern Ocean to describe plankton volume on a regional and seasonal basis. Hopkins (1971) similarly sampled to 2000 m in the Pacific sector (~75^{o}W-160^{o}W), obtaining 375 Bé net samples and found biomass distributions to be broadly comparable, both regionally and seasonally with Foxton's work. Important findings from both of these studies were that within the top 1000 m, seasonal variation in plankton biomass is marginal and also that increases in biomass were observed in the region of the Polar Front (PF). However, Foxton (1956) recognised that the N70V was poor in terms of catching krill which are particularly abundant south of the Polar Front, in the Antarctic Zone (AZ). Important studies by Hopkins and co-workers (e.g. Hopkins, 1985; Hopkins and Torres, 1988; Hopkins et al., 1993a) have investigated the biology and trophic ecology of the water column, including the deeper water

74 horizons in the Weddell Sea and adjacent marginal ice-zones (MIZ), as well as providing
75 community descriptions and insights into plankton diversity down the water column.
76 Atkinson and Sinclair (2000) used *Discovery* samples to assess the extent of seasonal
77 migration among the plankton and to clarify zonal distributions. Ward et al. (1995, 2006) and
78 Ward and Shreeve (1999) documented seasonal changes in community distribution and
79 biomass down to 1000 m around South Georgia and Marrari et al. (2011) investigated the
80 vertical distribution of zooplankton and habitat partitioning in the deeper water column in the
81 Marguerite Bay region of the Western Antarctic Peninsula (WAP).

82 Over the last 20 or so years, numerous studies have defined Southern Ocean plankton
83 community structure (e.g. Hosie, 1994; Errhif et al., 1997; Pakhomov et al., 2000, Ward et al.
84 2003, 2006). This has given us a near consistent view of epipelagic communities which are
85 bounded by the physical gradients and discontinuities often found at frontal zones. What is
86 presently unclear is whether such distinctions between plankton communities exist within the
87 mesopelagic and what patterns of diversity are discernible with respect to water mass and
88 depth. Studies of the mesopelagic (200-1000 m) elsewhere have emphasised that it is here
89 that processes govern the efficiency by which particulate organic carbon is transported to the
90 sea floor (Tréguer et al., 2003; Steinberg et al., 2008; Robinson et al. 2010) although we
91 generally know little regarding the abundance, biomass and vertical structure of the major
92 taxa involved. In the Southern Ocean Hopkins and Torres (1988) found diversity increased
93 below the epipelagic in the Weddell Sea, and Hopkins et al. (1993a, b) have shown that depth
94 was an important factor in determining spatial distance in an ordination of a series of samples
95 taken in the Scotia Sea MIZ in winter. A recent paper on diversity in the Arctic Ocean has
96 also shown depth to be a major structuring element for species distributions and communities
97 (Kosobokova et al., 2011 and references therein).

Extensive sampling of the mesopelagic rarely takes place these days, largely on grounds of cost. Fortunately, *Discovery Investigations* routinely sampled the Southern Ocean to 1000 m with the N70V net and many of these sets, taken ~80 years ago, are still available for study. The aim of this investigation was to examine the basic properties (abundance, species composition and diversity) of a series of plankton samples taken during 5 transects completed by *Discovery Investigations* along 80°W in the Pacific sector just west of Drake Passage, with a further aim of examining the spatial variability (horizontal and vertical) of the plankton community structure. The transects, occupied between December 1933 and November 1934, crossed three zones of the Antarctic Circumpolar Current, extending from the AZ in the south, through the Polar Frontal Zone (PFZ) to the sub-Antarctic Zone (SAZ) in the north (Fig. 1).

In this region of the Southern Ocean, temperatures have risen faster than elsewhere in the Southern Hemisphere, with surface summer temperatures rising more than 1°C during the last part of the 20th century (Meredith and King, 2005). Such changes have been predicted to have detrimental effects on various marine species including Antarctic krill, a key species in the Southern Ocean foodweb with a known dependence on the physical environment (Atkinson et al., 2004), and marine benthos, which is also sensitive to temperature change (Peck et al., 2004). In investigating zooplankton distributions from samples collected 80 years ago, we are establishing what patterns were prior to subsequent ocean changes and potentially forming a baseline against which the future impacts of such physical change might be measured.

2. Method

2.1 Zooplankton sampling and processing

A total of 41 stations were occupied during a series of 5 transects completed during the *Discovery Investigations*. The transects extended from ~ 68°S to 55°S along 80° W and were investigated during December 1933, March, September, October and November 1934 (Fig. 1). The position, number and horizontal spacing of stations varied between transects (5-10 stations per transect, transect lengths of ~690-1400 km). From these stations, 248 plankton samples were taken with an N70V net used extensively during *Discovery Investigations* to obtain stratified plankton samples. Of these, 9 samples were not located in the Natural History Museum collections and were presumed missing. Others had suffered some spillage during capture and initial processing, as indicated on the sample labels. Although these latter samples were examined, species counts were not included in subsequent data analysis reducing the total number of stations to 39 and samples to 215.

Full details of the N70V net construction are given in Kemp et al. (1929), but briefly it was a 70 cm dia. ring-net with two grades of silk mesh; a forward section of 40 threads per inch (TPI) and a rear section of 74 TPI equivalent to ~195µm and 440 µm respectively (Ward et al. 2012), and a collar of ~6 mm knotted mesh. The net was deployed in an open state and lowered to the bottom depth of the horizon to be fished before being hauled vertically upwards at a rate of 1 m sec^{-1}. Net closure was accomplished by use of a messenger sent down the wire at a predetermined time which triggered a closing mechanism as the net reached the upper depth of the fished horizon. This released the net bridles allowing a rope encircling the net and attached to the closing mechanism to throttle the net. Dependent on water depth, up to six samples were obtained as follows: 50 m to surface, 100–50 m, 250–100 m, 500–250 m, 750–500 m and 1,000–750 m. A full suite of vertical net samples was carried out in ~1.5-2hr.

144 The samples were taken almost 80 years ago and preserved in formalin. As might be
145 expected, overall condition was variable and not very good in the main. Crustaceans were
146 generally intact, although brittle, and internal tissue was often absent. Specimens of the
147 copepod *Calanoides acutus* had been removed from many samples and preserved separately.
148 A record of numbers removed was appended to the label in each jar, although the stage
149 structure of the absent fraction is unknown. Appendicularians were also often difficult to
150 identify because of tissue deterioration and thecosome pteropods likewise. Chaetognaths
151 were generally represented only by their jaws with the soft body tissue having dissolved
152 away. Numbers were therefore estimated by counting jaws and dividing by 2. Further
153 information on chaetognath species composition and other elements of the catch was obtained
154 from digitised records of photographs taken of *Discovery* logbook pages pertaining to each
155 haul (data provided by Andrew Mackey). Four species of chaetognaths were identified in
156 these logbooks, *Eukrohnia hamata* and 3 species of the genus *Sagitta*; *S. gazellae*, *S. maxima*
157 and *S. planctonis.* A comparison of *Discovery* logbook entries with jaw counts indicated that
158 overall, jaw counts underestimated abundance by ~10% (average jaw counts as a proportion
159 of *Discovery* counts = 0.91 (±0.781)). However not all logbook entries were consistent in
160 recording chaetognath numbers and a number of blank entries were apparent although
161 chaetognaths were present in the corresponding samples. For the sake of completeness we
162 have therefore decided to use abundance data generated from jaw counts/2 .
163 Initially samples were looked at in their entirety and rare and/or large specimens removed and
164 counted. Samples were then split successively using a folsom splitter until the resultant
165 aliquots were estimated to contain between 100-200 individuals which were again identified
166 and counted. Finally, further splitting took place to produce aliquots from which counts of the
167 smaller and more numerous size fractions were made. Both aliquots from each final split
168 were counted. An average of 753 (±297) individuals were counted per sample and, across all

169 samples, a total of 212 taxa /species /stages were identified (see Web appendix). Flow meters
170 were not used by *Discovery Investigations* and volume swept has been estimated from net
171 diameter and the depth of the water column that each net fished through. Thus, ~19 m^{-3} of
172 water was swept in a 50 m vertical tow, ~58m^{-3} in 150 m tow, and ~ 96 m^{-3} in a 250 m tow.
173
174 *2.2 Oceanography*
175 Temperature and water for salinity analysis were obtained from each station with
176 Ekman reversing bottles fitted with protected and unprotected reversing thermometers.
177 Thermometers were scaled to 0.1^{o}C and data presented in the station lists to two decimal
178 places. Salinity was analysed by titration against silver nitrate of known strength using
179 potassium chromate as an indicator (Kemp et al., 1929).
180 We used water mass properties at each of the *Discovery* stations to locate the
181 positions of the sub-Antarctic Front (SAF) and Polar Front (PF) on each transect, enabling
182 stations to be classified into three zones of the Antarctic Circumpolar Current (ACCZ): the
183 SAZ, PFZ and AZ. The frontal locations were determined from potential temperature-
184 salinity curves and confirmed with vertical sections of potential density along the transects
185 (Orsi et al, 1995; Read et al, 1995). Two transects (March and December) sampled south of
186 the southern ACC front but this front was not used to group stations in subsequent analyses.
187 *2.3 Statistical analysis*
188 PRIMER (v6) (Clarke and Gorley, 2006) was the principal statistical package used to
189 analyse the species-by-samples dataset. Routines were carried out on the species by stations
190 data matrix using log (x+1) transformed standardised data (ind. m^{-3} or ind.m^{-2}(0-1000 m)), to
191 determine Bray-Curtis similarities before undertaking hierarchical clustering of data into
192 sample groups (CLUSTER), and ordination (Multi dimensional scaling (MDS)). Analysis of
193 similarity (ANOSIM) was used to test for differences between resultant groups. ANOSIM

194 operates on the resemblance matrix and is approximately analogous to standard univariate
195 analysis of variance (ANOVA). Similarity percentages (SIMPER) was used to examine
196 taxonomic contributions towards group structure.

197 The PAST statistical package (Hammer et al. 2001), was used investigate species
198 diversity and specifically to undertake sample rarefaction (Mao tau) on the data converted
199 into a presence or absence matrix with respect to depth horizon. Rarefaction generates the
200 expected number of species in a small collection of *n* samples drawn at random from the
201 large pool of *N* samples (Gotelli and Colwell, 2001). The shape of the curve is steep at first
202 and then tends to plateau as only the rare species remain to be sampled. Rarefaction curves
203 generated from the present study were mostly beyond the steep phase but had yet to reach the
204 plateau phase. Therefore, we extrapolated the curves to determine (i) the expected number of
205 taxa within each depth interval and (ii) the level of sampling effort required to identify 90%
206 of this number of taxa. Both a 3-parameter power function and Michaelis-Menten function
207 were fitted to the rarefaction curves, with the former achieving the best levels of fit
208 (R^2>0.99). The power functions were then extended to three times the original sample size
209 (from ~36 to 108 samples) for each depth interval, following Colwell et al. (2004). The
210 rarefaction curves and extrapolations for each depth interval were plotted together for
211 comparative purposes.
212

213 **3. Results**

214 *3.1 Physical conditions along the transect*

215 Surface and subsurface positions of the fronts were located between the same station
216 pairs on all transects, with very few stations showing evidence of interleaving that is often
217 seen close to fronts. Our classification agrees with that of Foxton (1956) who partitioned

plankton standing crop into sub-Antarctic and Antarctic zones, although we additionally define the PFZ (Table 1). At the southernmost stations of each of the transect passes, temperature in the top 100 m of the water column was always less than 0 ^{o}C. At the northernmost stations at the same depth, temperature ranged from ~2.7—7.75 ^{o}C. A latitudinal increase of 1 ^{o}C per 155-200 km within the top 100 m was recorded for each transect, with temperature increasing northwards. The range of the average temperature calculated for the upper 100 m along each transect varied from 4.46 ^{o}C on the shortest transect (November) to 8.49 ^{o}C on the longer one (March). As expected, this near-surface temperature range was much larger (by a factor of 4.25 on average) than that recorded at 1000 m. Within all five transects, the difference between the minimum and maximum temperature at 1000 m was only 2.15 ^{o}C.

3.2 Mesozooplankton abundance by depth

Initially we calculated abundance (ind. m^{-3}) within each depth horizon and present these data as medians across all months and ACCZs (Table 2, Fig. 2). Median abundance within the top 100 m was significantly higher than in horizons deeper than 250 m (Kruskal–Wallis H=106.44, p=0.00). Abundance declined down the water column such that below 750 m the median was ~4% of that in the near-surface layers. Within depth horizons, monthly variation in range was greater (absolute and relative) in surface horizons than deeper (factor of 3-4 in top 50 m, 2-3 in 100-50 m and <2 in 250-100 m). Below 250 m the range was <1 and broadly equal across months.

3.3 Month vs ACCZs

There are some gaps in the data matrix when considering abundance with respect to ACCZ by month, which makes it difficult to get a strictly comparable view of monthly mesoplankton distributions by ACCZ (Table 1). Data from the SAZ are absent in November

and the PFZ is represented by only one sample in November and March. We have therefore plotted data showing variation in abundance across months and depth zones (ie ACCZs pooled) and also by variation across ACCZ and depth (ie months pooled). In the former (Fig 3a), the trend was for near-surface abundance to increase from September through till December and then decline slightly by March. In depth horizons below 100 m, no systematic change was observed across months, with the range of values tightly constrained compared to the upper 100 m. Below 250 m, abundance was reduced in each successive depth horizon by almost half in many cases. The ratio of the median abundance in the top 100 m to that in the deepest horizon varied from ~8-31 times across months. Pooling stations by ACCZ, irrespective of time of year (Fig. 3b), indicated that there was a greater range of values within the near-surface AZ compared to elsewhere. Deeper horizons (>500 m) once again appeared quite similar in overall abundance, irrespective of region. The high abundances seen in the near-surface waters of the AZ were due to the presence of limacinid pteropods during December. Median abundance and biomass by depth and ACCZ are presented in Table 2. Sample biomass was estimated from settled volumes provided by Foxton (1956) who included these samples along 80°W in an estimation of zooplankton standing stock in the Southern Ocean. Foxton provided data as displacement volumes (cm^{-3}) which we have converted to wet/dry mass assuming that 1 cm^{-3} equals 1 g wet weight and that dry weight represents 10% of this (see Hopkins 1971). Estimated biomass (wet mass mg m^{-3}) largely reflects patterns of abundance. Summed over the water column, median wet mass (gm^{-2}, 0-1000 m) was uniform, ranging from ~16 g in the AZ and SAZ to ~20 g in the PFZ. Dry mass using the 0.1 conversion advocated by Hopkins (1971) is therefore ~1.6-2.0 gm^{-2} (0-1000 m) across all ACCZs.

3.4 Spatial structure within the sample set

Clustering and multi-dimensional scaling (MDS) of Bray-Curtis similarities (latter not presented) showed that depth was by far the strongest factor in separating samples (Fig. 4). Three main clusters were apparent which could be classified as epipelagic (mainly samples taken in the top 100 m), upper mesopelagic (mainly samples from 100-250 m and 250-500 m horizons) and lower mesopelagic (mainly depths >500 m). Analysis of similarity (ANOSIM) to determine the extent to which the main clusters reflected depth was carried out using sample depth zone as a factor. A value of R= 0.66 (p=0.001), indicated that there was indeed a strong case for viewing the water column as broadly divisible into 3 horizons irrespective of ACCZ. We also tested whether month or time of sampling (day or night) had any significant influence on the clustering and found that both had much lower, yet still significant, values of R (R = 0.23, p=0.001 for month; R = 0.03, p=0.046 for day/night). The larger magnitude of R (which is an absolute measure of differences between groups, as compared with the p level, which is influenced by sample size) for depth shows that differences occasioned by month are slight in comparison with depth.

3.5 Community analysis

Although depth clearly dominated the way in which the sample specific dataset clustered, we also wished to determine the extent to which ACCZ might be a factor in horizontal variability. For the 27 stations which had a full complement of samples down to 1000 m (see Table 1), species stages were aggregated within species resulting in 171 species/taxa and abundance (ind. m^{-2}, 0-1000 m). Data were log (x+1) transformed, before clustering, MDS and subsequent routines were again carried out. We also wished to ascertain whether 'plankton communities' could be defined in waters >500 m deep. By restricting our analysis to the two deepest horizons fished by the N70V we increased the number of stations available for analysis from 27 to 33. However our first iterations of the 0-1000 m data matrix identified the strong influence on defining communities played by seasonal migrants (see

291 Atkinson 1988) and smaller, predominantly epipelagic species such as *Oithona similis*.
292 Therefore we first removed these to produce a species list that better reflected the deepwater
293 fauna (see legend Fig. 5). Following the removal of seasonal migrants and small near-surface
294 copepods, a total of 156 taxonomic categories remained. We examine these analyses in turn.

295 *0-1000 m*-- A plot of the MDS ordination on the 0-1000 m data set is presented in Fig
296 5a. At the 73% similarity level station groups comprised an AZ group (9 stns), an AZ/ PFZ
297 group (11 stns) and a predominantly SAZ grouping (7 stns).

298 *500-1000 m*-- By restricting our analysis to the two deepest horizons fished by the
299 N70V, we increased the number of stations available for analysis from 27 to 33. On this
300 occasion we observed two major groupings at ~72% similarity, the first of predominantly AZ
301 and PFZ stations and the second a diverse group of PFZ and SAZ stations (Fig. 5b).

302 A summary of ANOSIM performed on these data is presented in Table 3. Global R
303 for both ordinations was significant and among the pairwise comparisons of the ACCZs the
304 strongest difference was between AZ/SAZ. The value of R for the AZ/PFZ and PFZ/SAZ
305 pairwise comparisons more than halved (Table 3). This is consistent with the MDS plots
306 (Figs 5a-b) which suggest that stations along the transect form a continuum, with the spatial
307 extremes of AZ and SAZ stations differing most. We have therefore used the output from
308 ANOSIM and defined station groups with respect to ACCZ for subsequent analysis, rather
309 than trying to account for temporal and other differences in the data. The MDS plots
310 generally show stations thus identified as occupying different parts of the ordination.

311 We then ran the similarity percentages routine (SIMPER) to ascertain which
312 species/taxa were most responsible for within group structure. For the 0-1000 m ordination,
313 the small abundant species contributed most to within group similarity and between group
314 dissimilarity. In table 4 we have presented the 10 species/taxa contributing most to the above

for the 3 groupings identified by MDS (Fig. 5a), making a combined total of 20 species. Between 50-57% of within group similarity was accounted for by the tabulated taxa and ~40% of between group dissimilarity. Species/taxa so identified showed a range of distributions and abundances and overall the PFZ stations had the greatest average abundance of plankton (mean ~8.5 $x10^4$ ind. m^{-2} 0-1000 m, see table 5) although not significantly greater than the other two groups. Among species that often contributed most to dissimilarity between station groups were seasonal migrants including *Calanoides acutus*, *Calanus simillimus* and *Subeucalanus longiceps* and species that were widely distributed throughout the water column such as *Ctenocalanus* spp. and *Oithona similis*. The former species are seasonal migrants that spend spring/summer in near-surface waters and reside in deeper waters for the rest of the year. However, differences in the timing of life-cycles with respect to latitude means they are not uniformly distributed with respect to depth over the length of the transect.

In the 500-1000 m MDS plot (Fig. 5b) stations were once again broadly arrayed across the ordination. The pairwise comparisons of ACCZs carried out within ANOSIM showed a greater difference between the AZ and SAZ than of either with the PFZ (Table 3). In this case the PFZ/SAZ groupings were not significantly different and we have therefore pooled these before undertaking SIMPER. Again smaller copepod species proved to be the greatest contributors to within group structure. All except two of the first 10 taxa defining within group similarity and between group dissimilarity was the same in each of the two ACCZ groupings (20 taxa in total), with only the rank order changing (Table 6). A number of the deeper dwelling taxa, including the copepods *Metridia curticauda*, *Mormonilla* sp., *Paraeuchaeta biloba* and Scolecithriciid copepodites, as well as Siphonophora and *Thysanöessa* spp. were particularly important in defining dissimilarity between groups.

3.6 Seasonality in the mesopelagic

One of the questions we wished to answer was whether seasonal changes in abundance could be detected in the deeper depth horizons. We have presented 'spring' (Sept/Oct/Nov) and 'summer' (Dec/Mar) abundances of the 20 most abundant taxa (excluding seasonal migrants) in the 500-1000 m depth horizons across all ACCZs (Table 7). Overall there was a suggestion that one or two taxa were more abundant in summer than spring (e.g. *Oncaea* spp., *Metridia lucens* and *Paroithona* sp.) but only *Spinocalanus* spp.was significantly different and the majority of taxa showed very little difference between our seasonal groupings. However, given the length of the transect, there are likely to be 'seasonal' differences observed when comparing stations at one end with another. Within the Scotia Sea, Ward et al. (2004, 2006), have found differences in population age of biomass dominants *Calanoides acutus* and *Rhincalanus gigas,* to be as much as 3 months and possibly more, over transects of similar lengths, sampled quasi-synoptically. The possibility that grouping all stations together might be aliasing seasonality was investigated by looking for 'seasonal differences' within ACCZs.

We grouped 500-1000 m samples according to season, as before, but undertook comparisons within the AZ, and the PFZ/ SAZ ACCZs combined. The majority of ANOVA comparisons showed no difference between seasons. The most significant differences (5/40) were found in the AZ for Chaetognatha, *Paraeuchaeta antarctica* and Ostracoda where spring averages were all greater than summer ($p<0.05$). Among PFZ and SAZ stations, Chaetognaths (Spr<Su) and *Spinocalanus* spp. (Spr<Su) were significantly different. None of the taxa which showed significant seasonal differences in one ACCZ showed them in the other.

3.7 Diversity

The results of the rarefaction analysis are illustrated in Figure 6. The curves represent taxa numbers by depth, pooled across all ACCZs based on between 35-37 samples in each

365 depth horizon. Diversity increased systematically with depth, although the two deepest
366 horizons were virtually indistinguishable. None of the curves reached a plateau indicating
367 that diversity was underestimated. The slope of the curves was broadly identical for the 3
368 horizons within the top 250 m but steeper below 500 m, indicating a greater level of
369 undersampling of the total number of taxa at deeper depths. We have extrapolated the curves
370 for each horizon to 108 samples (approximately tripling the original sampling size within the
371 limits suggested by Colwell et al., 2004) to estimate the number of taxa expected at that
372 sampling intensity. The number of taxa observed in our analysed sample sets was between
373 70-80% of the estimated number based on 108 samples. To obtain 90% of the total taxa
374 predicted at 3 times the present sample size would require sample size to be doubled to
375 between 70 and 80 samples.

376 We have also plotted the median number of species/taxa found within each depth
377 horizon with respect to ACCZ (Fig. 7). The overriding pattern is of an increase with depth
378 across all ACCZs down to 500 m as well as from south (AZ) to north (SAZ). At depths >500
379 m, species numbers in all but the SAZ dropped somewhat. Further, we performed a stepwise
380 regression on the number of taxa recorded in each sample using depth, ACCZ and month as
381 predictors. This analysis clearly showed that depth alone was the most important factor
382 influencing diversity (r^2 adj = 0.60), with the fit being improved by ACCZ and month
383 (r^2=0.71, Mallows CP = 4.0). Overall plankton diversity was highest in the SAZ.

384 Across all depths, the mean number of taxa in the 0-1000 m water column with
385 respect to ACCZ was significantly greater in SAZ stations than elsewhere (Table 8). To
386 illustrate the general trends in the vertical and horizontal distributions of the major taxa, we
387 have plotted the median abundances (ind. m^{-3}) of families and groups with respect to depth
388 and ACCZ (Fig. 8). Within copepod families, trends were apparent both with depth and
389 across ACCZs. The Calanidae (*Calanoides*, *Calanus*, *Neocalanus*), Clausocalanidae

(*Clausocalanus*, *Ctenocalanus*, *Microcalanus*) and Oithonidae (*Oithona*, *Paroithona*) are all copepod families that were essentially more abundant within the surface 100 m. In the case of the Calanidae, this was largely due to the presence of younger stages during the summer months. To a greater or lesser extent, calaniids are interzonal migrants and spend a good proportion of the late summer and winter at depth, coming back into the surface layers in spring to reproduce (Andrews, 1966; Atkinson, 1991; Voronina, 1972). The distributional 'tail' reflects overwintering/overwintered stages distributed down to 1000 m. Within the Clausocalanidae, *Ctenocalanus* spp. was largely responsible for the increased abundance in the upper 100 m and *Microcalanus pygmaeus* below this. Within the Oithonidae, *Oithona similis* was largely responsible for the extremely high abundances in the surface 100 m with the less abundant *O. frigida* and *Paroithona* lying deeper. The Eucalaniids were most abundant in the 100-250 m zones with the two most abundant and widespread interzonal species (*Rhincalanus gigas* and *Subeucalanus longiceps*) spread down the water column with a tendency to be more abundant at northern stations. Ostracoda were widely distributed within the top 500 m but also occurred down to 1000 m. A number of families tended to peak within the 50-100 m and 100-250 m depth horizons e.g. Scolecitrichidae, Euchaetidae, Metridinidae, Aetideidae and Augaptilidae, whereas the Heterorhabdidae, Spinocalanidae, Phaennidae and Lucicutidae were generally more abundant below 500 m. A summary of the distribution of principal copepod families shown in the figure with respect to ACCZ is given in Table 9. Here the number of species identified across all ACCZs is given along with the number found within each defined ACCZ. A total of 102 copepod species were identified in the course of analysis although a number of copepod families such as the Oncaeidae, and Spinocalanidae and other non copepod taxa such as the Ostracoda and Siphonophora, were not resolved to species level and will certainly contain more species that are likely to have

414 distinct regional distributions. The overall pattern of copepod distribution indicated that
415 ~10% more copepod species were found within the SAZ compared to the AZ.
416
417 **4. Discussion**
418 *4.1 Sampling methodology*
419 Given that the samples were collected 80 years ago at a time when navigational and
420 oceanographic equipment were less technically advanced than today, we first discuss how
421 this might have impacted upon sample collection and our subsequent interpretation. In a pre-
422 satellite era, ships' navigation and positioning away from land was dependent upon celestial
423 sightings and, between times, dead reckoning. Practical accuracy would therefore have been
424 to the nearest nautical mile, far short of the level of accuracy achieved by the Global
425 Positioning System (GPS) today. However, this does not directly influence our interpretation
426 of data as we are dealing with an oceanographic context determined from the temperature and
427 salinity data rather than from geographical coordinates. Seawater properties were determined
428 from water samples taken with Ekman reversing bottles. The sampling depth of these bottles
429 was estimated from a metering sheave on the hydrographic gantry and checked against depth
430 determined from protected and unprotected thermometers located on some of the bottles. In
431 the *Discovery* station lists (Anonymous, 1942) nominal metered depth can be checked against
432 actual depth for some of the bottles. The two estimates are generally to within a few meters of
433 one another even at depths of 3-4 km indicating that we can be confident of the hydrographic
434 sampling. Temperature is given to 2 decimal places (less than the 4 decimal places generally
435 used today) although the thermometers used were described as being scaled to 0.1^{o}C (Kemp
436 et al., 1929). Given that we used the data to determine whether a front lay between relatively
437 widely spaced stations, this level of accuracy is sufficient for our interpretation.

438 It is more difficult to assess whether the nominal net depth is as indicated, as no
439 independent estimate of depth was apparently undertaken. However, even though wire angles
440 must have deviated from the vertical at times, the accuracy of the deeper water bottle
441 sampling suggests that depth determination during vertical net sampling may also have been
442 reasonably accurate. Wire deviations are expected to be greater in bad weather. Data on wind
443 speed at each of the 41 stations indicates that, at the vast majority (~88%), the Beaufort scale
444 was ≤ 4 at the commencement of operations further suggesting that this may not have unduly
445 influenced net depths.

446 Both bottle sampling and netting were accomplished in a relatively short space of
447 time. Generally, two stations were worked each day commencing at around 9am and 8pm.
448 Netting operations of all types took ~ 4 hours to complete, with an N70V net series to 1000 m
449 generally taking ~1.5-2 hours. A series of Ekman water bottles could be hauled to the surface
450 at ~5.5 min per 1000 m of wire out although would have been deployed at a somewhat slower
451 rate. Thus time on station was not excessive and the zooplankton and hydrographical
452 sampling would be spatially related. It is unlikely that, at any one station, hydrographic
453 sampling was undertaken in one water mass and zooplankton sampling in another.

454 The nets were deployed open to the lower point of the sampled horizon and then
455 hauled vertically upwards before being closed which raises the question of catch
456 contamination, particularly of deeper horizons with surface contaminants. Previous studies
457 have shown that contamination can take place when nets are deployed in this way and
458 plankton are captured as the net jerks upwards when the ship rolls (Grice and Hulsemann
459 1968, Harding 1972). However, *Discovery Investigations* deployed this net over an
460 accumulator spring which would have tended to have minimised this problem (Atkinson
461 1988). Additionally, many of the particularly abundant species that occur throughout the
462 water column such as *Oithona similis* and *Ctenocalanus* spp. and which are more likely to be

potential contaminants are known to be seasonal migrants and/or widely distributed within the water column (Atkinson 1988). Although contamination cannot be quantitatively examined, the orders of magnitude lower abundances seen in all of the deeper horizons (Figs 2, 3) suggest it is minimal. The isolated occurrences of deeper species in near-surface nets can in all probability be attributed to insufficient washing down of nets between hauls.

4.2 Abundance and biomass

The pattern of mesozooplankton abundance decreasing with depth was similar across all months. Abundance was highly variable in the surface 100 m although greatly exceeded that in the deeper water column. Although somewhat lower overall in the SAZ, both abundance and biomass were not significantly different between ACCZs when viewed over the whole sampled water column. Higher zooplankton abundance near the PF has previously been observed, particularly where phytoplankton biomass was also high (Foxton, 1956, Pakhomov et al., 2000, Dubischar et al., 2002). In our study area, elevated chlorophyll levels are today generally restricted to the near continental shelf region (Fig 1), well south of the position of the PF. It is also likely that, regionally, zooplankton standing stock is lower here than in many other parts of the ACC because of the low primary production seen in the region of 80°W (Fig. 1). Abundance and biomass in the depth horizons below 250 m generally exhibited less variation whether pooled by ACCZ or month.

Biomass estimates along 80°W derived from Foxton's (1956) data were somewhat lower (~1.6 to 2.0 g dw m^{-2}) than estimates determined by Hopkins (1971) for the Pacific sector, which were 2.67 and 2.58 g dw m^{-2} (0-1000 m) for the Antarctic and sub-Antarctic regions respectively. However Foxton excluded gelatinous zooplankton from his determinations and the two estimates may be closer than first appears. Different net performance could also be a factor (see Table 3 Atkinson et al., 2001). Samples for Hopkins' study were taken with a net mesh size of 202 µm. Recent research has shown systematic

488 differences between N70V catches and a 200 µm bongo net, with the latter catching ~3 times
489 more (by abundance) than the former which translates to ~1.6 times greater biomass (Ward et
490 al., 2012).

491 *4.3 Community analysis*

492 Both MDS ordinations suggested a continuum of stations and species distributions,
493 rather than groups divided by distinct boundaries. This probably reflects the greater number
494 of taxa pooled over a greater depth and the ironing out of seasonal differences when the data
495 were pooled across months. In the deeper ordination (Fig. 5b) community structure was less
496 clear cut, with PFZ stations appearing close in ordination space to AZ and SAZ stations. This
497 may in part be due to manipulating the data by removing seasonal migrants and restricting the
498 analysis to defined depth horizons but also to the lower and more uniform abundances found
499 at depth as well as the rarity of many species. Numerous studies have previously identified
500 plankton communities within the ACC (Errhif et al., 1997; Hunt and Hosie 2005; Pakhomov
501 et al., 2000; Ward et al., 2003). These have generally been based on samples taken from the
502 epipelagic and are very often defined by changes in species abundance rather than by a
503 fundamentally different species composition. In these studies, the PF has generally
504 represented a significant community boundary but, for mesopelagic species, it is less clear cut
505 (Atkinson and Sinclair, 2000). In the deeper horizons where seasonality is less pronounced
506 than in the near-surface, abundances are more uniform and many of the copepod species in
507 particular, whilst widespread, are uncommon. Additionally, previous studies have been
508 largely synoptic rather than using data that have been pooled from September through to
509 March.

510 Mackintosh (1934), Chiba et al. (2001) and Mackey et al. (2012) have all underlined
511 the importance of temperature in determining the distributions of many species of Southern

Ocean plankton. Atkinson and Sinclair (2000) have also argued that there is little evidence that the PF forms a biogeographic barrier to the distribution of many species owing to their wide-spread distribution at depth. Our analysis also reflects the wider distribution of many species (Tables 4 and 6). The relatively low values of the R statistic for the AZ/ PFZ and the PF/SAZ pairwise comparisons versus its high values for the AZ/SAZ comparison (Table 3), suggests that the PFZ represents a transition zone. The PFZ has been characterized by the presence of a mixture of sub-Antarctic, sub-tropical and Antarctic species and as such represents a biogeographic ecotone-type community (Pakhomov et al., 2000). There is also no doubt that many species do have distributions that are relatively unaffected by the presence of the PF. Many of the horizontal gradients at ACCZ boundaries are weak relative to vertical gradients and are too weak to limit species distributions which tend to form a continuum, characterised by core regions and regions of expatriation (Angel 1997). Nevertheless, many other species exhibit step changes in abundance in passing from one side of a front to the other and watermass preferences are marked (Boltovskoy et al., 1999). In the wider South Atlantic, Boltovskoy et al. (1999) plotted species distributional boundaries against latitude and found that by far the highest number occurred in the transition zone between the subtropical and sub-Antarctic around 30-40^{o}S. This warm-cold water transition was stronger than the second highest found in the vicinity of the PF.

4.4 Seasonality

Despite pronounced seasonality in the near-surface Antarctic pelagial (Clarke 1988; Smetacek et al., 1990) we found no indirect evidence that this was also apparent in the mesopelagic. Abundance and biomass varied little below 250 m (Table 2) and testing by ACCZ only 5 of 40 taxa/species seasonal abundance comparisons were significantly different, suggesting that seasonal differences were not widespread within the 500-1000 m horizons. In many oceans, seasonal flux of organic material to the deep-sea has been detected

537 at many thousands of metres depth (Billett et al., 1983; Asper et al., 1992). In the North
538 Atlantic, Koppelmann and Weikert (1999) found evidence that, below 1000 m, many
539 species/taxa had summer:spring ratios of >1, suggesting a reproductive response to the spring
540 bloom, particularly in the upper bathypelagic zone (1050-2250 m). This increase was
541 pronounced among calanoid copepods and in particular the Metridinidae which increased by
542 a factor of 13.5 between spring and summer. In regions where blooms are largely absent, it
543 was suggested that such responses would not be detected (Kopplemann and Weikert, 1999).
544 They cite summer biomass profiles from the Madeira Abyssal Plain (Roe, 1988), where
545 spring blooms do not occur, as being similar to pre-bloom spring profiles from the
546 BIOTRANS site in the temperate northeast Atlantic where their study was carried out.

547 In this part of the Southern Ocean, levels and periodicity of primary production may
548 also be important. Our contemporary composite of ocean colour (Fig. 1) shows that highest
549 levels of chlorophyll are generally found south of the transect locations and may be
550 associated with the retreating ice-edge. To the north of this, chlorophyll is uniformly low
551 (<0.5 mg l^{-1}). Production patterns have probably not changed dramatically over the years
552 because the transect lies upstream of the main sources of iron input into the ACC in this
553 sector, namely shelf deposits from the Antarctic Peninsula and topographically induced
554 upwelling (Park et al., 2010). Data on the presence of phytoplankton in the 80°W samples are
555 given by Foxton (1956) (Table 11c). December and March samples from the AZ contained
556 phytoplankton in the near-surface layers which implies that 'summer' stations in the AZ in
557 1933/34 were only just experiencing a bloom, suggesting that deep-water fauna would in any
558 case have had no time to respond to this burst of production. A reproductive response later in
559 the year (early winter onwards) may explain why spring abundance of some species was
560 greater than during summer. Interannual variability also may be partly responsible insofar as

561 the summer grouping (Dec. 1933 and Mar. 1934) precede rather than succeed the spring
562 grouping (Sept, Oct, Nov 1934) and so effectively different cohorts were being assessed.

563 *4.5 Diversity*

564 Within this study a number of taxonomic categories were unresolved into species. Our
565 'lumping' of species manifested itself variously at the level of phylum, e.g. Chaetognatha,
566 Ctenophora; class or order e.g. Ostracoda, Siphonophora, Appendicularia; family or genus
567 e.g. Lucicutiid copepodites, *Oncaea* spp. etc. Of the taxa identified, copepods were the most
568 highly resolved to species level. Reasons for this variously included the state of preservation
569 of some elements of the samples, expedience in wishing to analyse a large number of samples
570 in a timely manner and levels of taxonomic expertise. Nonetheless some clear patterns
571 emerged. Rarefaction analysis highlighted the relationship of increasing diversity with depth
572 when species presence/absence data from all ACCZs were pooled with respect to depth (Fig
573 6). This was also to an extent mirrored in the clustering of station data with respect to depth
574 (Fig 4) which effectively partitioned the water column across all ACCZs into 3 distinct
575 horizons. The rarefaction curves from the two deepest horizons corresponding to the lower
576 mesopelagic (*sensu* Fig. 4) indicate a greater diversity and have a steeper slope than the
577 shallower depth-horizons indicating a different rate of species accumulation. It should be
578 borne in mind that each deep sample represents 5 times the amount of water swept per sample
579 in the upper two horizons in the top 100 m. However, the slope of the species accumulation
580 curve was different and even with an extrapolated sample number (equivalent to a greater
581 volume of water swept) diversity never approaches that of the deeper horizons. Modern net
582 sampling of the deep water column is usually undertaken with larger nets than the N70, using
583 oblique rather than vertical hauls and generally sampling a greater volume of water. This
584 would undoubtedly influence the rate of accumulation of species per haul but the relative
585 pattern between the different horizons is unlikely to change dramatically.

586 It is difficult to summarise patterns of diversity across such a heterogenous group as
587 plankton. Some groups are taxonomically better investigated than others, using both
588 traditional morphology and modern molecular techniques such as genetic bar coding (Bucklin
589 et al. 2011) but, at a wider scale, the polar and sub-polar biomes are less rich in species across
590 many groups than their tropical and subtropical counterparts (Angel et al., 2007; Boltovskoy
591 et al., 1999; Woodd-Walker et al., 2002). In near-surface samples, Woodd-Walker et al.
592 (2002) have demonstrated the large-scale spatial variation in taxonomic richness of copepod
593 genera across the whole Atlantic Ocean. Higher diversity was apparent in the tropics and
594 sample eveness and diversity also reduced dramatically around 40°S and towards the poles.
595 This has been attributed to the former possessing a relatively stable environment where
596 seasonal changes are minimal, allowing for a largely retentive system in which primary and
597 secondary producers are closely coupled and diversity is characteristically high (Conover,
598 1979; Longhurst and Pauly, 1987). Polewards, seasonality increases and production and
599 consumption become increasingly uncoupled and diversity is lower. Increasing diversity
600 with depth may therefore reflect the relative stability of the lower part of the mesopelagic in
601 contrast to the seasonal breakdown of the thermocline and the winter overturning of the upper
602 water column (Woodd-Walker et al., 2002). At a smaller spatial scale our analysis suggested
603 that slightly more copepod species were present in the SAZ than in either the AZ or PFZ.
604 This was in large measure through higher species numbers within the families Aetideidae and
605 Augaptilidae being found in the SAZ (Table 9). However, based on the wider literature,
606 Razouls et al. (2005-2012) record 47 and 39 members of the Aetideidae and 27 and 20
607 members of the Augaptilidae in the AZ and SAZ respectively. Our samples only recovered a
608 relatively small proportion of these totals which reflects sampling effort, regional bias and
609 overall rarity of many of the deeper dwelling species (see E-Table). Large-scale physics in
610 the form of mesoscale eddies (Nowlin and Klinck 1986) may also influence diversity by

611 introducing species polewards or in some cases equatorwards across the PF. Based on the
612 wider literature extending to the entire Southern Ocean, Razouls et al. (2005-2013) estimate
613 that the number of copepod species occurring in all Antarctic waters totals 295 compared to
614 275 reported for the sub-Antarctic. They have also suggested that ~80% of copepod species
615 observed in the sub-Antarctic are immigrants and originate from sub-tropical and temperate
616 zones. It is possible that these form 'pseudo-populations' (Razouls et al., 2005-2013) and
617 many of these may already be at the limits of their distributional ranges. Other taxonomic
618 groups such as Amphipoda, Ostracoda and Salpidae, appear to have a greater number of
619 species in the SAZ whereas others such as euphausiids, chaeotognaths and some radiolarians
620 appear more evenly distributed (Boltovskoy et al., 1999).

621 *4.6 Long-term change*

622 Profound physical changes have occurred in the Southern Ocean in the intervening 80
623 or so years since *Discovery Investigations*, At the WAP, close to the 80°W transect, climate
624 change has been rapid. Atmospheric temperatures have risen by ~3°C since 1951 (Vaughan et
625 al. 2003) and extensive glacial retreat has occurred (Cook et al., 2005). The surrounding
626 ocean temperature has also increased by ~1°C in summer (Meredith and King 2005), and sea-
627 ice duration and cover has declined in this region (Cavalieri and Parkinson 2008). The
628 potential and actual impacts of such changes are being recognised in various parts of the
629 marine ecosystem, (eg Atkinson et al., 2004; Ducklow et al., 2007; Clarke et al., 2007;
630 Forcada et al 2006; Schofield et al., 2010) and are generally complex.

631 The transect along 80°W lies north and west of the WAP and is largely north of the
632 seasonal sea-ice zone. Ocean warming throughout the region has not been uniform with depth
633 and, along with decreased salinity, is greater in near-surface waters (Meredith and King,
634 2005; Böning et al., 2008). Because of warming and freshening, Böning et al. (2008) estimate
635 that density surfaces between the PF and SAF at 800-1000 m have been displaced southwards

50–80 km in the last 40 years and perhaps 2-3 times this distance at the surface. This may imply a southwards displacement of frontal zones but this is likely to be difficult to detect against the natural background variation in the position of the ACC fronts (Moore et al., 1999; Venables et al., 2012). Plankton distributions frequently show strong temperature dependence in the Southern Ocean (Mackintosh, 1934; Chiba et al., 2001; Mackey et al., 2012). Simplistically, as a consequence of warming, we might expect a southwards penetration of some 'warmer' water species and a contraction in the range of cold water species as predicted by Mackey et al. (2012) for macrozooplankton. This seems plausible as Ward et al. (2004, 2006) have shown that, in extensive surveys of the Scotia Sea, mesoplankton, particularly copepods, were much less abundant in ice influenced waters. A polewards movement of the ice-edge may therefore progressively result in increased zooplankton diversity and abundance further south. However, many species have wide distributional ranges, occurring in all ACCZs sampled and over wide depth ranges and without the benefit of time-series data change is not going to be easy to detect (Ward et al., 2008, 2012; Mackey et al., 2012). Nonetheless, *Discovery* samples were taken over a large part of the Southern Ocean using the same sampling gear and provide a valuable resource with which to undertake comparisons on a regional basis and with contemporary collections.

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References

Acker, J. G., Leptoukh, G. 2007. Online Analysis Enhances Use of NASA Earth Science Data. Eos, Trans. AGU, 88, 14 -17.

Andrews, K. J., 1966. The distribution and life-history of *Calanoides acutus* (Giesbrecht). Discovery Report 34, 117-162.

Angel, M. V., 1997. Pelagic biodiversity, In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: Patterns and Processes, Cambridge University Press, pp. 35-68.

Angel, M. V., Blachowiak-Samolyk, K., Drapun I., Castillo, R., 2007. Changes in the composition of planktonic ostracod populations across a range of latitudes in the North-east Atlantic. Progress in Oceanography 73:60-78.

Anonymous,1942. Station list,1933–1935. Discovery Report 22, 1–196.

685 Asper, V. L., Deuser, W. G., Knauer, G. A., Lohrenz, S. E.,1992. Rapid coupling of sinking
686 particle fluxes between surface and deep ocean waters. Nature 357, 670-672.
687 Atkinson, A., 1988. The ecology and distribution of zooplankton around the island of South
688 Georgia, Antarctica. PhD thesis, Council for National Academic Awards. 260 pp.
689 Atkinson, A., 1991. Life cycles of *Calanoides acutus*, *Calanus simillimus* and *Rhincalanus*
690 *gigas* (Copepoda: Calanoida) within the Scotia Sea. Marine Biology 109, 79-91.
691 Atkinson, A., Sinclair, J. D., 2000. Zonal distribution and seasonal vertical migration of
692 copepod assemblages in the Scotia Sea. Polar Biology 23, 46-58.
693 Atkinson, A., Whitehouse, M. J., Priddle, J., Cripps, G. C., Ward, P., Brandon, M. A., 2001.
694 South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. Marine Ecology
695 Progress Series 216, 279-308.
696 Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock
697 and increase in salps within the Southern Ocean. Nature 432, 100-103.
698 Billett, D. S. M., Lampitt, R. S., Rice, A. L., Mantoura, R. F. C., 1983. Seasonal
699 sedimentation of phytoplankton to the deep-sea benthos. Nature 302, 520-522.
700 Boltovskoy, D., Gibbons, M., Hutchings, L., Binet, D., 1999. General biological features of
701 the South Atlantic. In: Boltovskoy, D. (Ed.) South Atlantic Zooplankton **1**: Leiden:
702 Backhuys, pp 1-43.
703 Böning, C. W., Dispert, A., Visbeck, M., Rintoul, S. R., Schwarzkopf, F. U., 2008. The
704 response of the Antarctic Circumpolar Current to recent climate change. Nature Geosciences
705 1, 864-869.
706 Bradford-Grieve, J. M., 1994. Pelagic calanoid Copepoda: Megacalanidae, Calanidae,
707 Paracalanidae, Mecynoceridae, Eucalanidae, Spinocalanidae, Clausocalanidae. New Zealand
708 Oceanographic Institute Memoir 102, 1-160.

709 Bradford-Grieve, J. M., 1999.The Marine Fauna of NewZealand: Pelagic Calanoid
710 Copepoda: Bathypontiidae, Arietellidae, Augaptilidae, Heterorhabdidae, Lucicutiidae,
711 Metridinidae, Phyllopodidae, Centropagidae, Pseudodiaptomidae, Temoridae, Candaciidae,
712 Pontellidae, Sulcanidae, Acartiidae, Tortanidae. NIWA Biodiversity Memoir 11, 1-268.
713 Bucklin, A., Steinke, D., Blanco-Bercial, L., 2011. DNA barcoding of marine metazoa.
714 Annual Review of Marine Science, 3, 471-508.
715 Cavalieri, D. J., Parkinson, C. L., 2008. Antarctic sea ice variability and trends, 1979–2006,
716 Journal of Geophysical Research, 113, *C07004, doi:*10.1029/2007JC004564.
717 Chiba, S., Ishimaru, T., Hosie, G. W., Fukuchi, M., 2001. Spatio-temporal variability of
718 zooplankton community structure off east Antarctica (90 to 160 ^{o}E). Marine Ecology
719 Progress Series 216, 95-108.
720 Clarke, A., 1988. Seasonality in the antarctic marine environment. Comparative Biochemistry
721 and Physiology B: Comparative Biochemistry 90, 461-473,

722 Clarke, A., Murphy E. J., Meredith, M., King, J. C., Peck, L. S., Barnes, D. K. A., Smith, R.
723 C., 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula
724 Philosophical Transactions of the Royal Society B. 362, 149-166.

725 Clarke, K. R., Gorley, R. N., 2006. PRIMER v6: User Manual/tutorial. Primer-E Ltd
726 Plymouth.

727 Colwell, S. K., Mao, C. X., Chang, J., 2004. Interpolating, extrapolating and comparing
728 incidence-based species accumulation curves. Ecology 85, 2717-2727.

729 Conover, R. J., 1979. Secondary production as an ecological phenomenon. In: Van der Spoel,
730 S., Pierrot-Bults, A.C. (Eds.). Zoogeography and Diversity in Plankton, Bunge Scientific
731 Publishers, Utrecht, pp 50-86.

732 Cook, A. J., Fox, A. J., Vaughan, D. G., Ferrigno, J. G., 2005. Retreating glacier fronts on the
733 Antarctic Peninsula over the past half-century. Science 308, 541-544.
734 David, P. M., 1955. The distribution of *Sagitta gazellae* Ritter-Zahony. Discovery Report 27,
735 235–278.
736 David, P. M., 1958. The distribution of the Chaetognatha of the Southern Ocean. Discovery
737 Report 29, 199–228.
738 Dubischar, C. D., Lopes, R. M., Bathmann, U. V., 2002. High summer abundances of small
739 pelagic copepods at the Antarctic Polar Front-implications for ecosystem dynamics. Deep Sea
740 Research II 49, 3871-3887.

741 Ducklow, H. W., Baker, K., Martinson, D. G., Quetin, L. B., Ross, R. M., Smith, R. C.,
742 Stammerjohn, S. E., Vernet, M., Fraser, W., 2007. Marine pelagic ecosystems: the West
743 Antarctic Peninsula. Philosophical Transactions of the Royal Society B, 362, 67-94.

744 Errhif, A., Razouls, C., Mayzaud, P., 1997. Composition and community structure of pelagic
745 copepods in the Indian sector of the Antarctic Ocean during the end of the austral summer.
746 Polar Biology 17, 418-430.
747 Forcada, J., Trathan, P. N., Reid, K., Murphy, E. J., Croxall, J. P., 2006. Contrasting
748 population changes in sympatric penguin species in association with climate warming. Global
749 Change Biology 12, 411–423.
750 Foxton, P., 1956. The distribution of the standing crop of zooplankton in the Southern Ocean.
751 Discovery Report 28, 193-235.
752 Gotelli, N., Colwell, R., 2001. Quantifying biodiversity: procedures and pitfalls in
753 measurement and comparison of species richness. Ecology Letters 4, 379-391.
754 Grice, G.D., Hulsemann, K., 1968. Contamination in Nansen-type vertical nets and a method
755 to prevent it. Deep-Sea Research 15, 229-233.

Hammer, Ø., Harper, D.A.T., Ryan, P. D., 2001. PAST: Paleontological Statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 9 pp

Harding, G. C. H., 1972. Ecological observations on North Atlantic deep-sea copepods. PhD Thesis, Dalhousie University, 201 pp.

Hopkins, T. L., 1971. Zooplankton standing crop in the Pacific sector of the Antarctic. Antarctic Research Series 17, 347-362.

Hopkins, T. L., 1985. The zooplankton community of Croker passage, Antarctic Peninsula. Polar Biology 4, 161-170.

Hopkins, T. L., Torres, J.J., 1988. The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. Polar Biology 9, 79-87.

Hopkins, T. L., Ainley, D.G., Torres, J.J., Lancraft, T.M., 1993a. Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). Polar Biology 13, 389-397.

Hopkins, T. L., Lancraft, T. M., Torres, J. J., Donnelly, J., 1993b. Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). Deep Sea Research 40, 81-105.

Hosie, G.W., 1994. The macrozooplankton communities in the Prydz Bay region, Antarctica. In: el-Sayed, S.Z. (Ed.) Southern Ocean Ecology, The Biomass Perspective. Cambridge University Press, pp 93-124.

Hunt, B. P. V., Hosie, G. W., 2005. Zonal structure of zooplankton communities in the Southern Ocean South of Australia: results from a 2150 km continuous plankton recorder transect. Deep Sea Research 52, 1241-1271.

Kemp, S., Hardy, A. C., Mackintosh, N. A., 1929. The Discovery Investigations, objects, equipment and methods. Part 2. The ships, their equipment and the methods used in research. Discovery Report 1, 151–222.

781 Koppelmann, R., Weikert, H., 1999. Temporal changes of deep-sea mesozooplankton
782 abundance in the temperature NE Atlantic and estimates of the carbon budget. Marine
783 Ecology Progress Series 179, 27–40.
784 Kosobokova, K. N., Hopcroft, R. R., Hirche, H-J., 2011. Patterns of zooplankton diversity
785 through the depths of the Arctic's central basins. Marine Biodiversity 41, 29-50.
786 Longhurst, A. R., Pauly, D., 1987. Ecology of tropical oceans. Academic press San Diego
787 CA, USA, 407 pp.
788 Mackey, A., Atkinson, A., Hill, S., Ward, P., Cunningham, N. J., Johnson, N., Murphy, E. J.,
789 2012. Antarctic macrozooplankton of the southwest Atlantic sector and Bellingshausen Sea:
790 baseline historical (*Discovery Investigations,* 1928-1935) distributions related to temperature
791 and food, with projections for subsequent ocean warming. Deep Sea Research II 59-60, 130-
792 146.
793 Mackintosh, N. A., 1934. Distribution of the macroplankton in the Atlantic sector of the
794 Antarctic. Discovery Report 9, 65-160.
795 Mackintosh, N. A., 1937. The seasonal circulation of the Antarctic macroplankton. Discovery
796 Report 16, 365-412.
797 Marrari, M., Daly, K. L., Timonin, A., Semenova, T., 2011. The zooplankton of Marguerite
798 Bay, western Antarctic Peninsula—Part II: Vertical distributions and habitat partitioning,
799 Deep Sea Research II 58, 1614-1629.
800 Meredith, M. P., King, J. C., 2005. Rapid climate change in the ocean west of the Antarctic
801 Peninsula during the second half of the 20th century. Geophysical Research Letters 32,
802 L19604, doi:10.1029/2005GL024042.
803 Moore, J. K., Abbott, M. R., Richman, J. G., 1999. Location and dynamics of the Antarctic
804 Polar Front from satellite sea surface temperature data. Journal Geophysical Research 104
805 (C2), 3059-3073.

806 Nowlin Jr., W. D., Klinck, J. M., 1986. The physics of the Antarctic Circumpolar Current.,
807 Reviews of Geophysics, 24, 469–491.
808 Ommaney, F. D., 1936. *Rhincalanus gigas* (Brady), a copepod of the southern
809 macroplankton. Discovery Report 5, 277-384.
810 Orsi, A. H., Whitworth, T., Nowlin Jr, W.D., 1995. On the meridional extent and fronts of the
811 Antarctic Circumpolar Current. Deep-Sea Research I 42, 641—673.

812 Pakhomov, E. A., Perissinotto, R., McQuaid, C. D., Froneman, P. W., 2000. Zooplankton
813 structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer
814 1993: Part 1. Ecological zonation. Deep Sea Research I 47, 1663-1686.

815 Park, T., 1978. Calanoid copepods belonging to the families Aetideidae and Euchaetidae
816 from Antarctic and Subantarctic waters. In: Pawson, D.L. (Ed.). Biology of the Antarctic
817 Seas VII, Antarctic Research Series 27. AGU Washington D.C., pp. 91-290.
818 Park, T., 1983. Calanoid Copepods of the Genus *Scaphocalanus* from Antarctic and
819 Subantarctic Waters. In: Kornicker, L.S. (Ed.). Biology of the Antarctic Seas XI, AGU,
820 Washington, D.C., pp. 75-127.
821 Park, T., 1993. Calanoid copepods of the genus *Euaugaptilus* from Antarctic and
822 Subantarctic waters, in Cairns, S.D., (Ed) Biology of the Antarctic Seas XXII, AGU,
823 Washington, D.C., pp. 1-48.
824 Park, J., Im-Sang, Oh., Hyun-Cheol, K., Sinjae Y., 2010. Variability of SeaWiFs
825 chlorophyll-*a* in the southwest Atlantic sector of the Southern Ocean: Strong topographic
826 effects and weak seasonality. Deep Sea Research 57, 604-620.
827 Peck, L. S., Webb, K. E., Bailey, D. M., 2004. Extreme sensitivity of biological function to
828 temperature in Antarctic marine species. Functional Ecology 18, 625-630.

829 Razouls C., de Bovée F., Kouwenberg J., Desreumaux N., 2005-2013. Diversity and
830 Geographic Distribution of Marine Planktonic Copepods. Available at http://copepodes.obs-
831 banyuls.fr/en [Accessed July 25, 2013]

832 Read, J. F., Pollard, R. T., Morrison, A. I., Symon, C., 1995. On the southerly extent of the
833 Antarctic Circumpolar Current in the southeast Pacific. Deep-Sea Research II, 42, 933-954.

834 Robinson, C., Steinberg, D. K., Anderson, T. R., Arístegui, J., Carlson, C. A., Frost, J. R.,
835 Ghiglione, J-F., Hernandez-León, S., Jackson, G. A., Koppelmann, R., Quéguiner, O.,
836 Ragueneau, O., Rassoulzadegan, F., Robison, B. H., Tamburini, C., Tanaka, T., Wishner, K.
837 F., Zhang, J., 2010. Mesopelagic zone ecology and biogeochemistry–a synthesis. Deep Sea
838 Research II 57, 1504-1518.

839 Roe, H. S. J., 1988. Midwater biomass proflles over the Madeira Abyssal Plain and the
840 contribution of copepods. Hydrobiologia 167/168, 169-181.
841 Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., Fraser,
842 W., 2010. How Do Polar Marine Ecosystems Respond to Rapid Climate Change? Science
843 328, 1520-1523.
844 Smetacek, V., Scharek, R., Nöthig, E. M., 1990. Seasonal and regional variation in the
845 pelagial and its relationship to the life history cycle of krill. In: Kerry, K.R., Hempel, G.
846 (Eds) Antarctic Ecosystems, Springer Berlin Heidelberg, pp. 103-114.
847 Steinberg, D. K., Cope, J. S., Wilson, S. E., Kobari, T., 2008. A comparison of mesopelagic
848 mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean.
849 Deep Sea Research II 55, 1615-1635.
850 Tréguer, P., Legendre, L., Rivkin, R.T., Ragueneau, O., Dittert, N., 2003. Water column
851 biogeochemistry below the euphotic zone. In: Fasham, M.J.R. (Ed.). Ocean Biogeochemistry

852 the role of the ocean carbon cycle in global change. Springer-Verlag Berlin Heidelberg New
853 York, pp. 145-156.
854 Vaughan, D. G., Marshall, G. J., Connolley, W. M., Parkinson, C., Mulvaney, R., Hodgson,
855 D. A., , King, J. C., Pudsey, C. J., Turner, J., 2003. Recent rapid regional climate warming on
856 the Antarctic Peninsula. Climatic change 60, 243-274.
857 Venables, H., Meredith, M. P., Atkinson, A., Ward, P., 2012. Fronts and habitat zones in the
858 Scotia Sea. Deep-Sea Research II 59-60, 14-24.
859 Voronina, N. M., 1972. The spatial structure of interzonal copepod populations in the
860 Southern Ocean. Marine Biology 15, 336-343.
861 Ward, P., Atkinson, A., Murray, A. W. A., Wood, A. G., Williams, R., Poulet S. A., 1995.
862 The summer zooplankton community at South Georgia: biomass, vertical migration and
863 grazing. Polar Biology 15, 195-208.
864 Ward, P., Shreeve R. S., 1999. The spring mesozooplankton community at South Georgia: a
865 comparison of shelf and oceanic sites. Polar Biology 22, 289-301.
866 Ward, P., Whitehouse, M., Brandon, M., Shreeve, R., Woodd-Walker R., 2003.
867 Mesozooplankton community structure across the Antarctic Circumpolar Current to the north
868 of South Georgia: Southern Ocean. Marine Biology 143, 121-130.
869 Ward, P., Grant, S., Brandon, M., Siegel, V., Sushin, V., Loeb, V., Griffiths, H., 2004.
870 Mesozooplankton Community Structure in the Scotia Sea during the CCAMLR Survey:
871 January-February 2000. Deep Sea Research II 51, 1351-1367.
872 Ward, P., Shreeve, R., Atkinson, A., Korb, B., Whitehouse, M., Thorpe, S. Pond, D.,
873 Cunningham, N., 2006. Plankton community structure and variability in the Scotia Sea:
874 austral summer 2003. Marine Ecology Progress Series 309, 75-91.

875 Ward, P., Meredith, M. P., Whitehouse, M. J., Rothery, P., 2008. The summertime plankton
876 community at South Georgia (Southern Ocean): Comparing the historical (1926/1927) and
877 modern (post 1995) records. Progress in Oceanography 78, 241-256.

878 Ward, P., Tarling, G.A., Coombs, S.H., Enderlein, P., 2012. Comparing Bongo net and N70
879 mesozooplankton catches: using a reconstruction of an original net to quantify historical
880 plankton catch data. Polar Biology 35, 1179–1186.

881 Wiebe, P. H., Ashjian, C. J., Lawson, G. L., Piñones, A., Copley, N. J., 2011. Horizontal
882 and vertical distribution of euphausiid species on the Western Antarctic Peninsula U.S.
883 GLOBEC Southern Ocean study site. Deep Sea Research II 58, 1630-1651.
884 Woodd-Walker, R. S., Ward, P., Clarke, A., 2002. Large-scale patterns in diversity and
885 community structure of surface water copepods from the Atlantic Ocean. Marine Ecology
886 Progress Series 236, 189-203.

887 Fig. 1. Composite satellite image showing mean chlorophyll *a* during the period September –
888 March 2004–2012, east of Drake Passage. White areas denote missing data due to
889 land/cloud/sea ice cover. Superimposed are *Discovery* station positions coded by month.
890 Shaded grey rectangles represent the limits within which the sub-Antarctic Front (SAF) and
891 Polar Front (PF) were found during these transects. The chlorophyll *a* data used in Fig. 1 are
892 MODIS-Aqua 9 km resolution, level 3 data provided by the NASA Goddard Earth Sciences
893 Data and Information Services Center (Acker and Leptoukh, 2007).
894

895 Fig. 2. Logged Mesozooplankton abundance (ind m^{-3}) with respect to depth. Data shown are
896 median plus interquartile range (box) and 10^{th} and 90^{th} percentiles (whiskers). Dots represent
897 outliers. Data have been pooled within depth horizons across ACC Zones.
898

899 Fig. 3. a) Mesozooplankton abundance (ind. m^{-3}) versus depth by month. Open symbols
900 represent individual data points, filled circles, median values by depth. Key for depth: 1 = 50-
901 0 m, 2 = 100-50 m, 3 = 250-100 m, 4 = 500-250 m, 5 =750-500 m, 6=1000-750 m.

902 b) Mesozooplankton abundance (ind.m^{-3}) versus ACC zone by depth. Open symbols
903 represent individual data points, filled circles, median values by ACC zone. Key for depth, as
904 for Figure 3. ACC zone abbreviations as Table 1.

905 Fig. 4. Results of nearest neighbour clustering on the Bray-Curtis similarity matrix containing
906 all sample data. Samples have been coded according to depth horizon. We have sliced the
907 cluster dendrogram at 70% similarity. At ≥70% similarity, the dendrogram has been
908 collapsed and stations are represented by symbols at the similarity level at which they first
909 became statistically indistinguishable. Red lines at <70% similarity extend from the point at
910 which the grouping became statistically indistinguishable from one another. Black lines
911 extending to the *x* axis are statistically dissimilar to other stations.

912

913 Fig. 5a) MDS ordination carried out on the 0-1000 m data matrix. Lines encircling stations
914 represent 73% similarity.

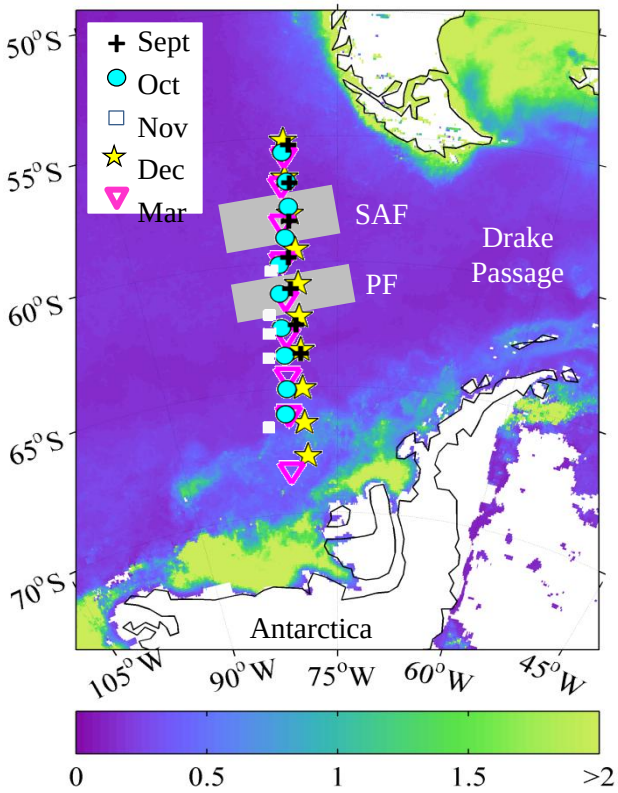
915 5b) MDS ordination carried out on the 500-1000 m data matrix with seasonal migrants
916 omitted (see below). Lines encircling stations represent 72% similarity.

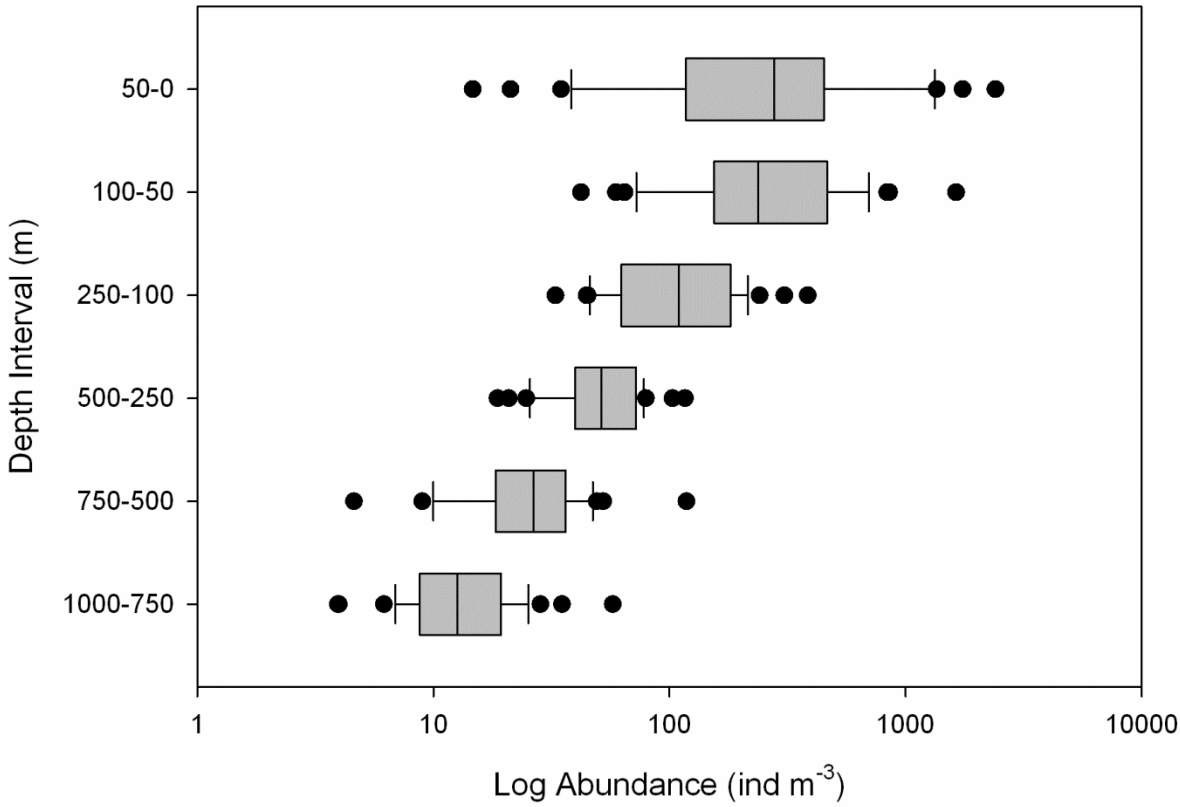
917 Open circles = AZ stations, filled triangles PFZ stations and open squares SAZ stations.

918 Taxa omitted from 500-1000m data matrix were *Calanoides acutus*, *Calanus simillimus*,
919 *Neocalanus tonsus*, *Rhincalanus gigas* plus nauplii, *Subeucalanus longiceps*, *Ctenocalanus*
920 spp. *Clausocalanus laticeps*, *Clausocalanus brevipes*, *Ctenocalanus/Clausocalanus*

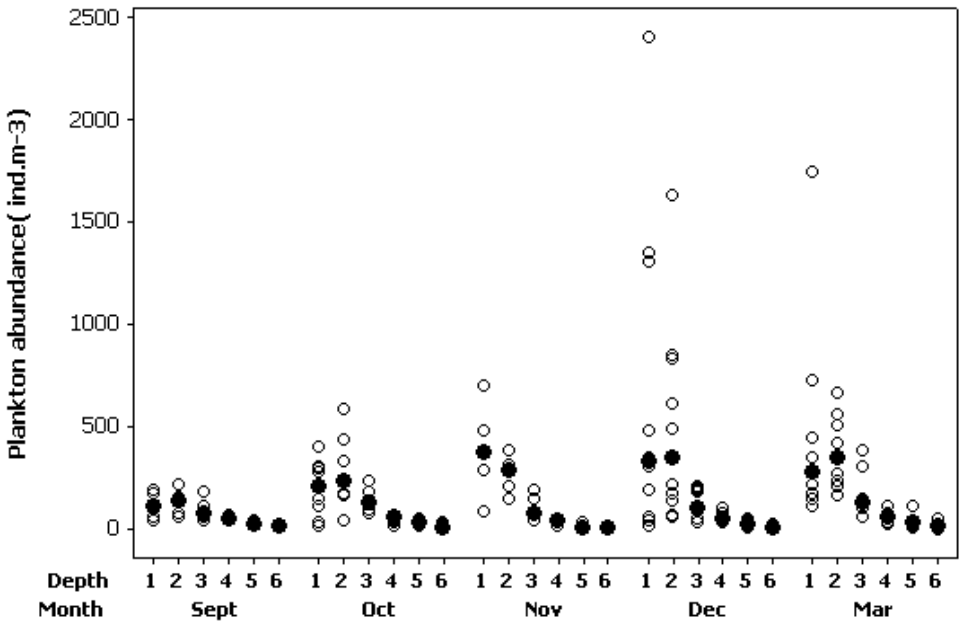
921 copepodites, *Scolecithricella minor*, *Oithona similis*, *Limacina helicina*, *Limacina retroversa*
922 and Appendicularia spp.

923 Fig. 6. Rarefaction curves based on a presence/absence species by depth matrix. Between 35-
924 37 samples were used from each depth horizon to construct the curves using the "Moa tau"
925 method (bold lines). A 3 parameter power function fitted to each rarefaction curve was then
926 extrapolated to 3 times the sample size (108 samples) following Colwell et al., (2004; fine
927 lines).
928 Fig. 7. Boxplot of median number of species/taxa in each depth horizon with respect to ACC
929 zone. Data shown are median plus interquartile range (box) and max and min (whiskers) * =
930 outlier. Depth coding as for Fig. 3.
931
932 Fig. 8. Median abundance (ind. m^{-3}) of major copepod families and other taxa by ACC zone
933 and depth. Data shown are median plus interquartile range (box) and max and min
934 (whiskers), * = outlier. Depth coding as for Fig. 3.
935

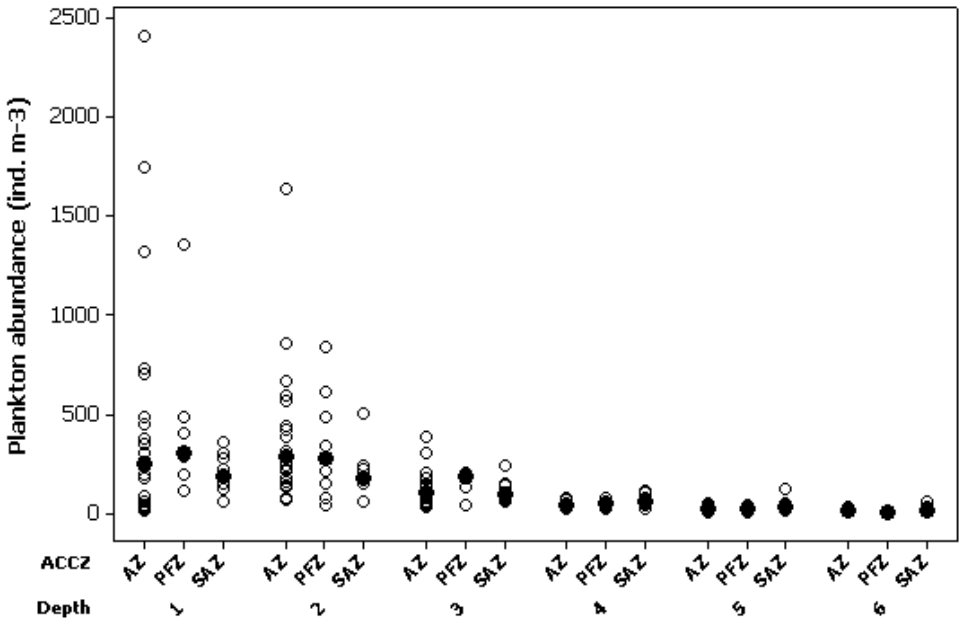

Sept
Oct
Nov
Dec
Mar
SAF
PF
Drake
Passage
Antarctica
50°S
55°S
60°S
65°S
70°S
105°W
90°W
75°W
60°W
45°W
0
0.5
1
1.5
>2

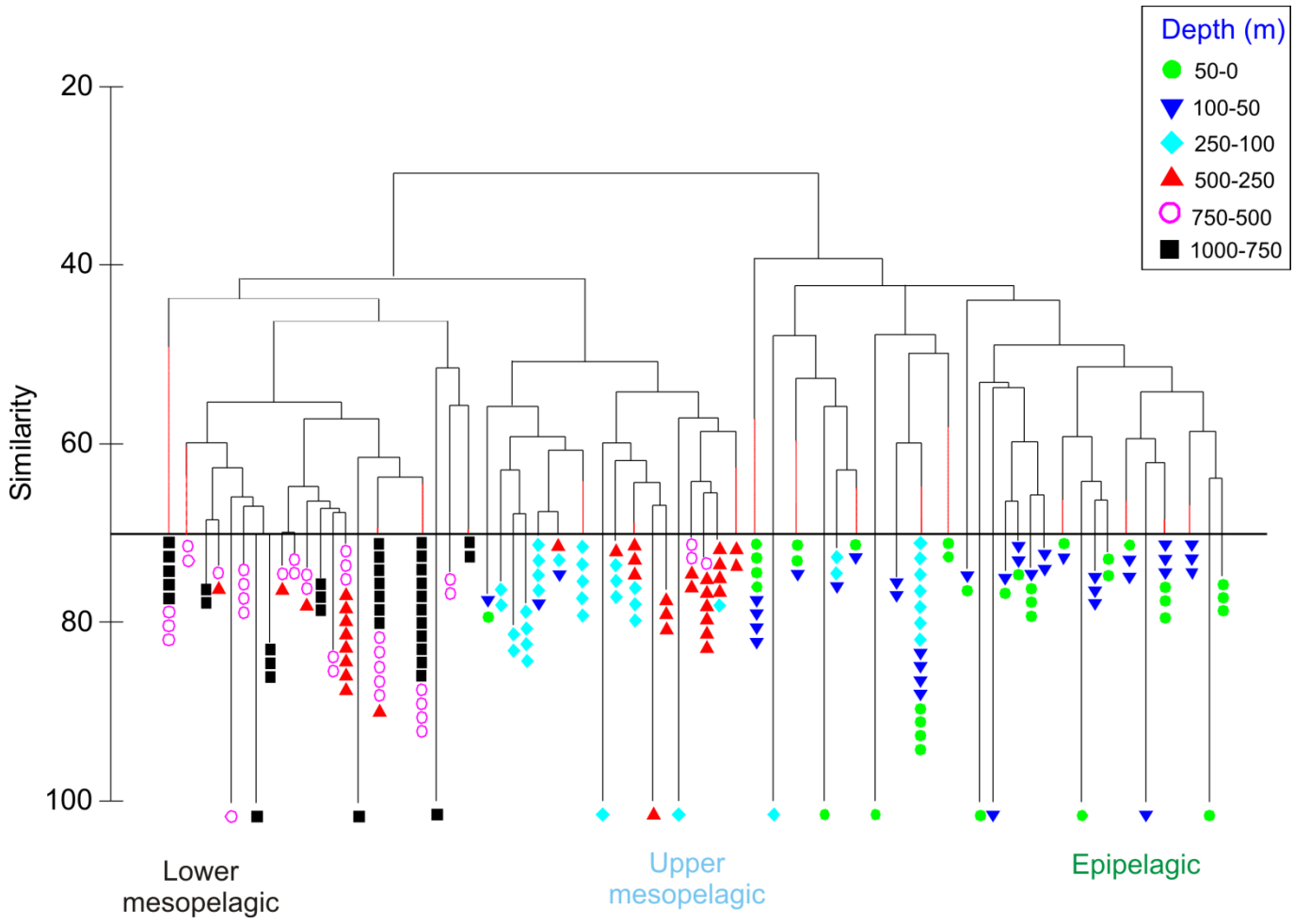

50-0
100-50
250-100
500-250
750-500
1000-750
Depth Interval (m)
1
10
100
1000
10000
Log Abundance (ind m-3)

3a

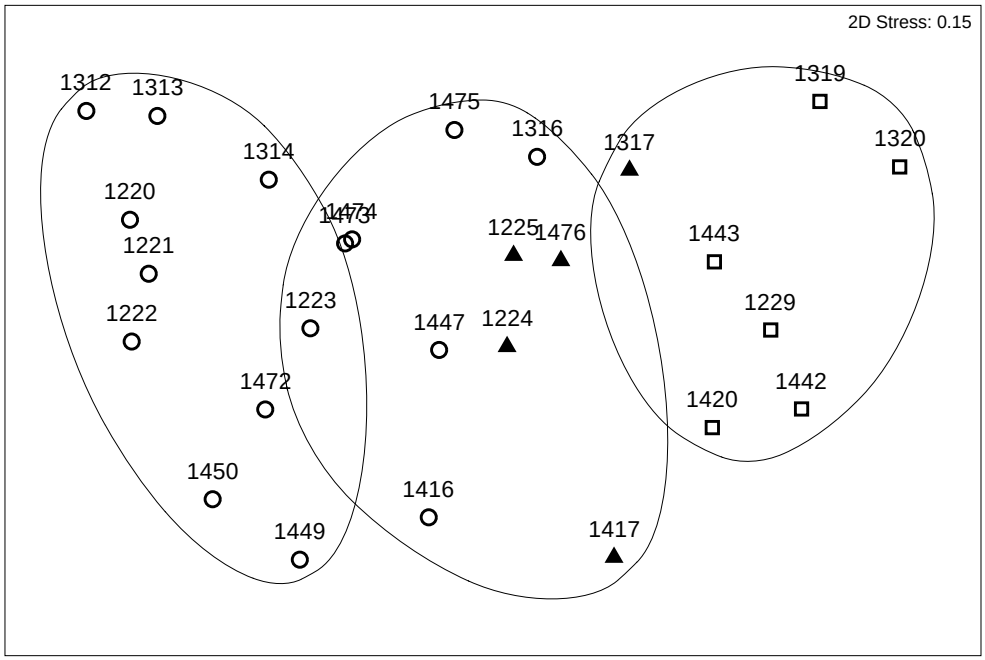

Plankton abundance(ind.m-3)
2500
2000
1500
1000
500
0
Depth 1 2 3 4 5 6 1 2 3 4 5 6 1 2 3 4 5 6 1 2 3 4 5 6 1 2 3 4 5 6
Month Sept Oct Nov Dec Mar

3b


Plankton abundance (ind. m-3)
2500
2000
1500
1000
500
0
ACCZ AZ PFZ SAZ AZ PFZ SAZ AZ PFZ SAZ AZ PFZ SAZ AZ PFZ SAZ AZ PFZ SAZ
Depth 1 2 3 4 5 6


Depth (m)
50-0
100-50
250-100
500-250
750-500
1000-750
Similarity
20
40
60
80
100
Lower mesopelagic
Upper mesopelagic
Epipelagic

5a


2D Stress: 0.15
1312
1313
1314
1220
1221
1222
1223
1472
1450
1449
1475
1316
1474
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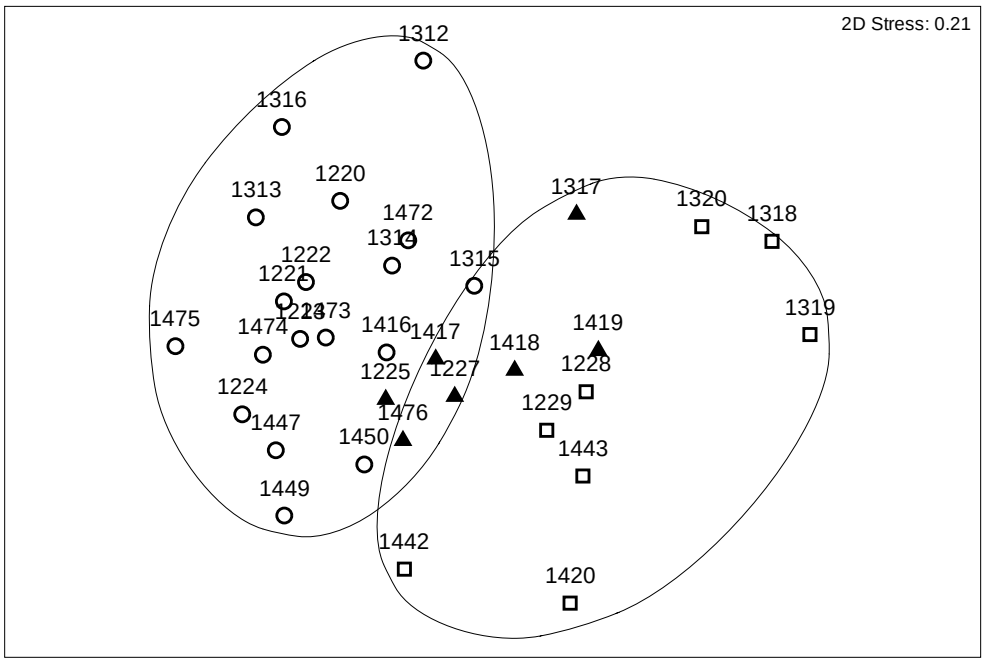
1319
1320
1443
1229
1420
1442

5b


2D Stress: 0.21
1312
1316
1313
1220
1472
1222
1221
1475
1474
1473
1416
1417
1315
1225
1227
1224
1447
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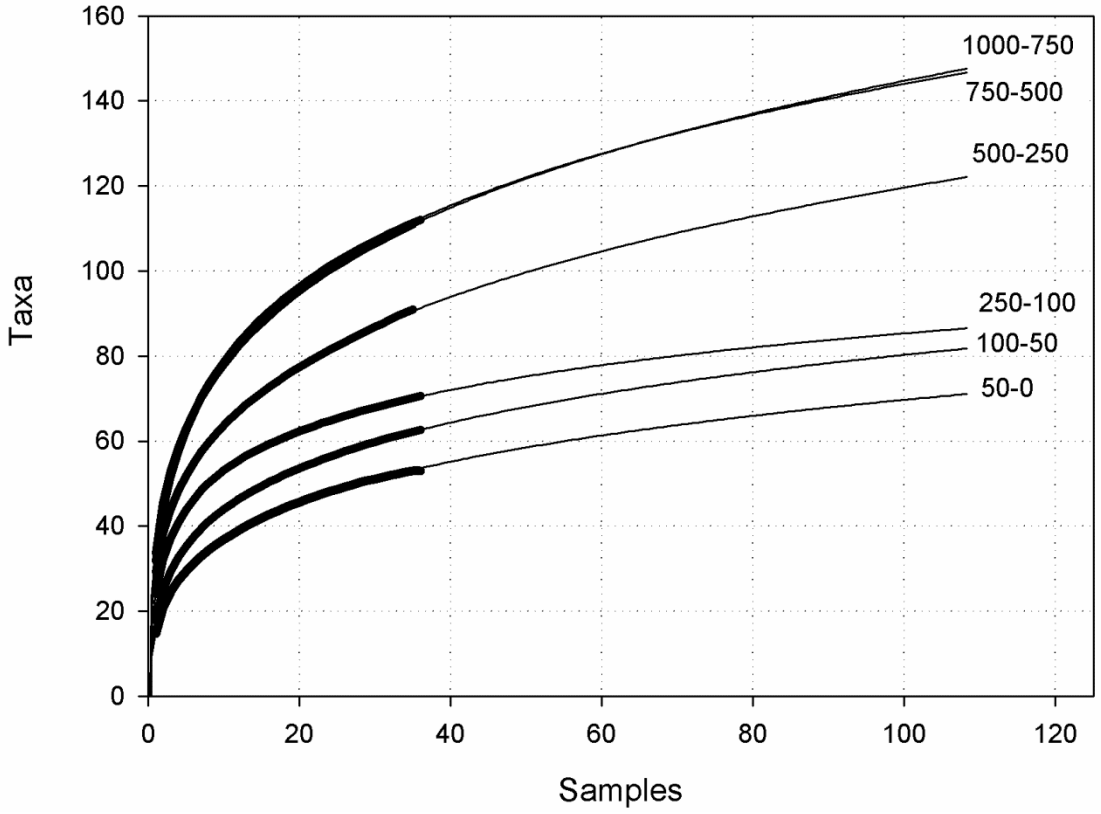
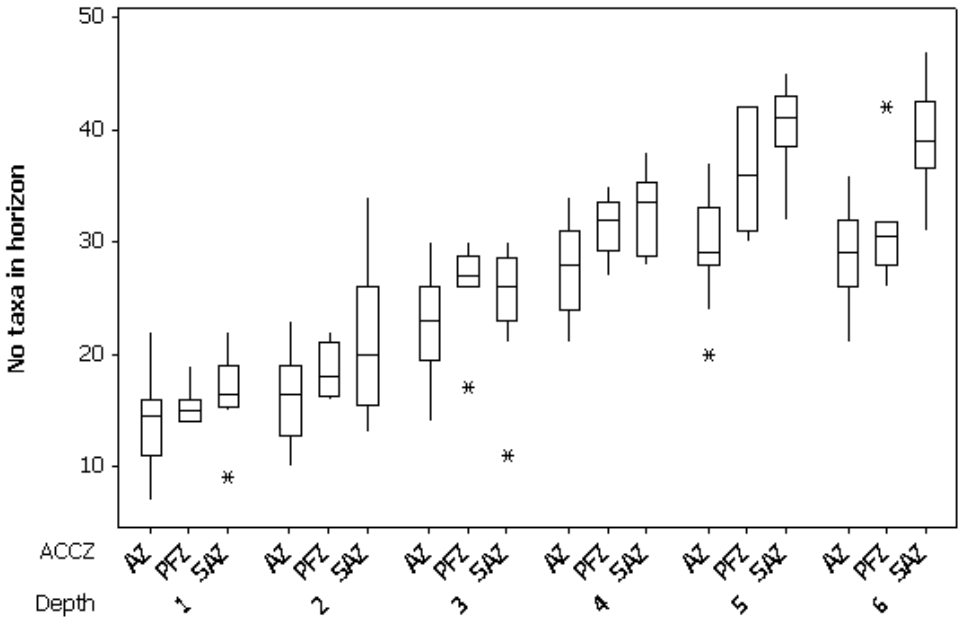
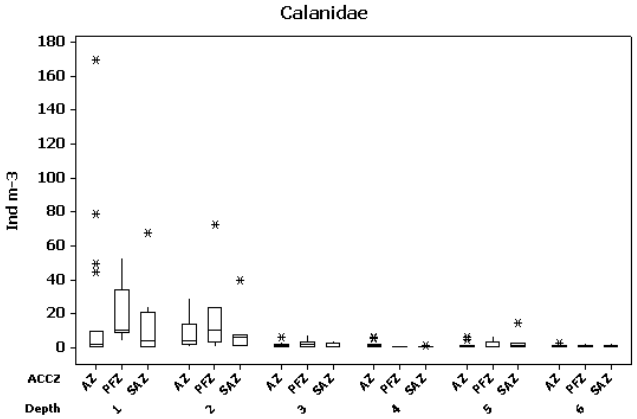
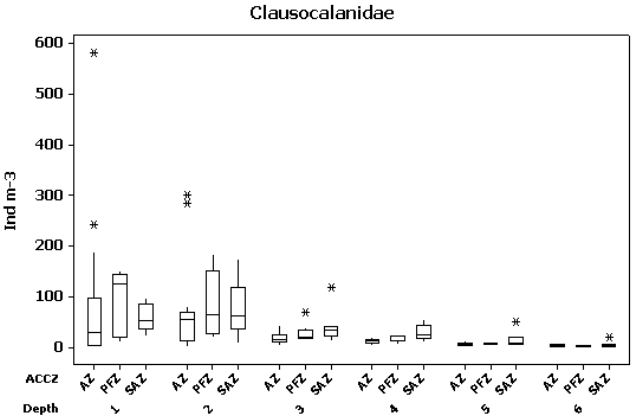
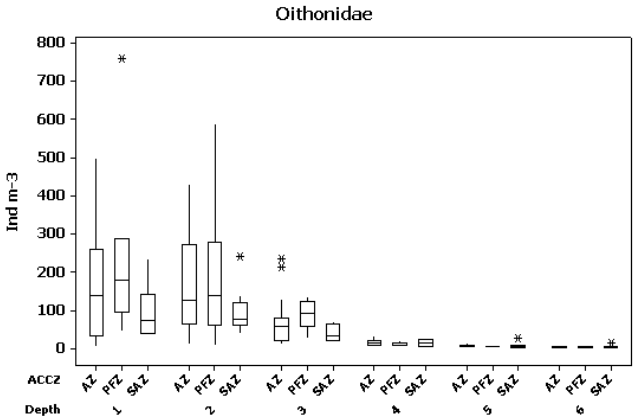
1443

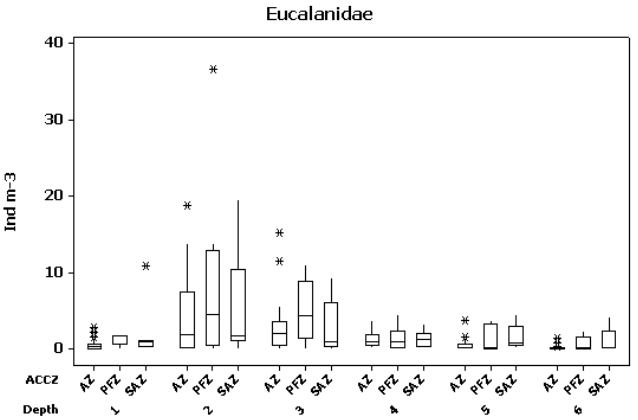

160
140
120
100
80
60
40
20
0
Taxa
0
20
40
60
80
100
120
Samples
1000-750
750-500
500-250
250-100
100-50
50-0

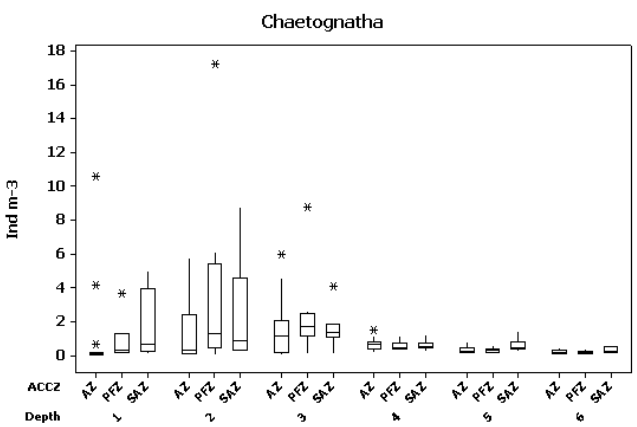

No taxa in horizon
50
40
30
20
10
ACCZ
AZ
PFZ
SAZ
Depth
1
2
3
4
5
6

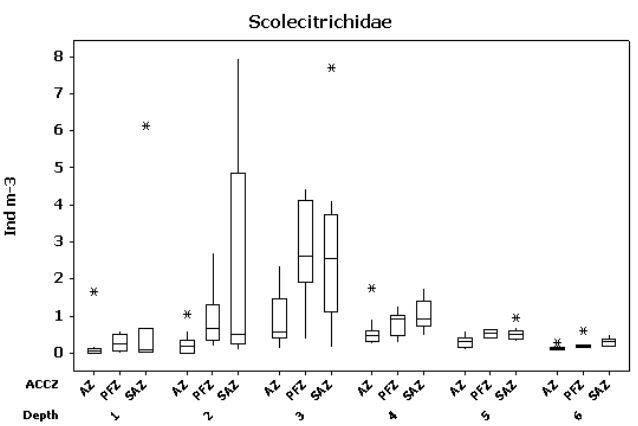

Calanidae
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

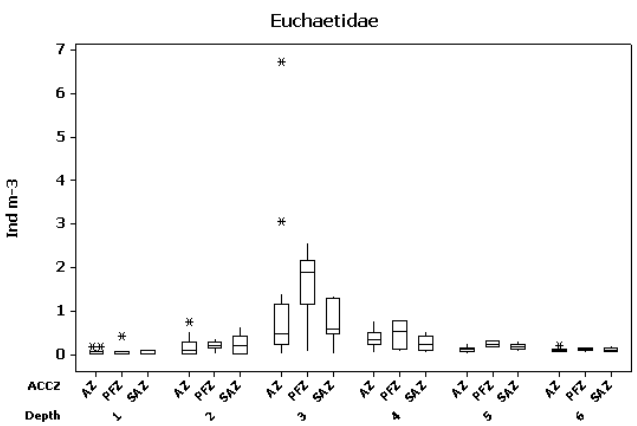

Clausocalanidae
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

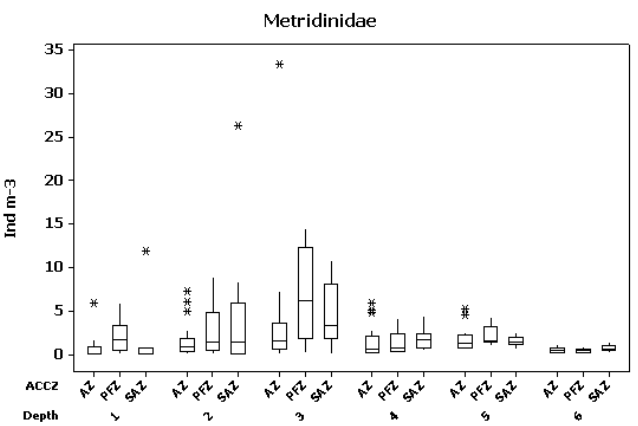

Oithonidae
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

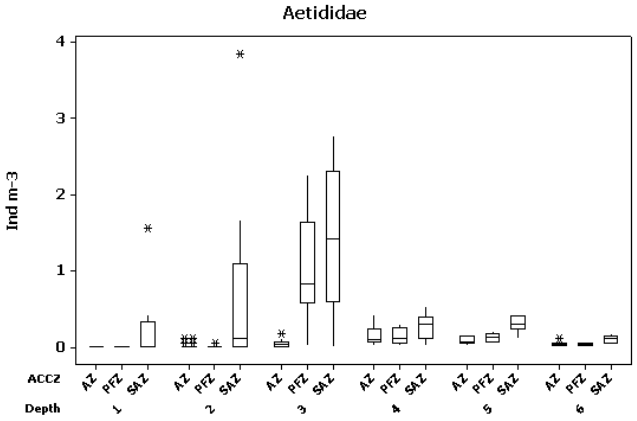

Eucalanidae
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

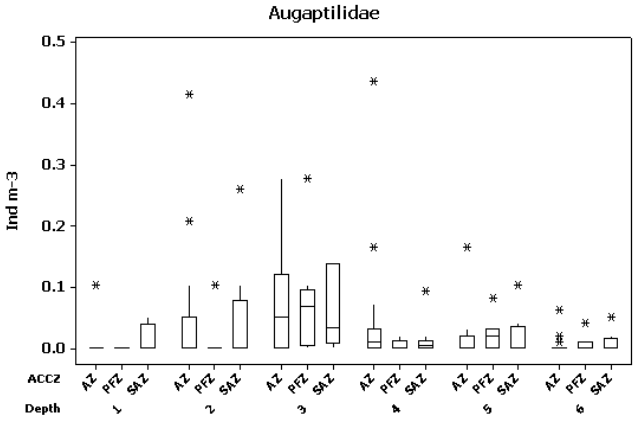

Chaetognatha
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

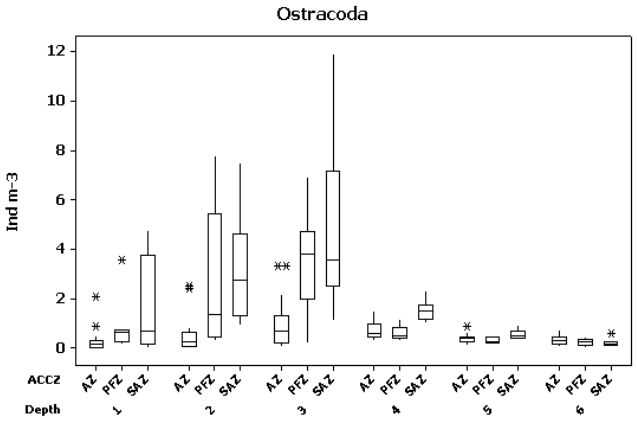

Scolecitrichidae
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

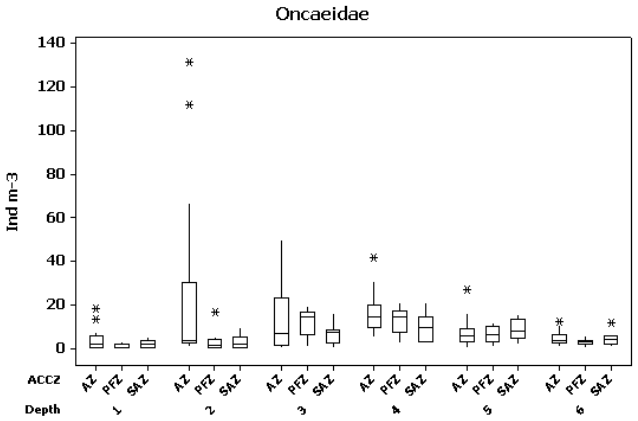

Euchaetidae
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

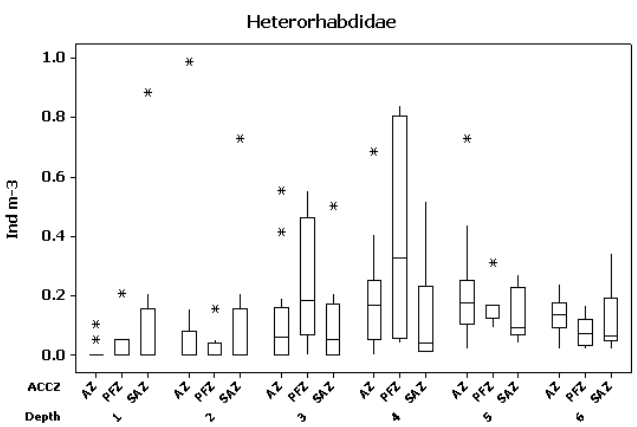

Metridinidae
Ind m-3
ACCZ
AZ PFZ SAZ
Depth
1 2 3 4 5 6

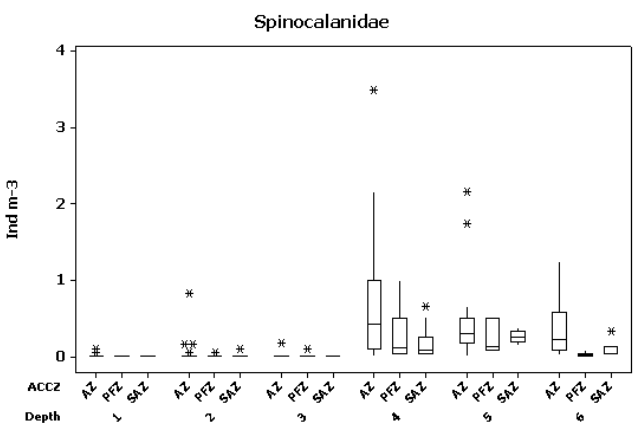

Aetididae
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6

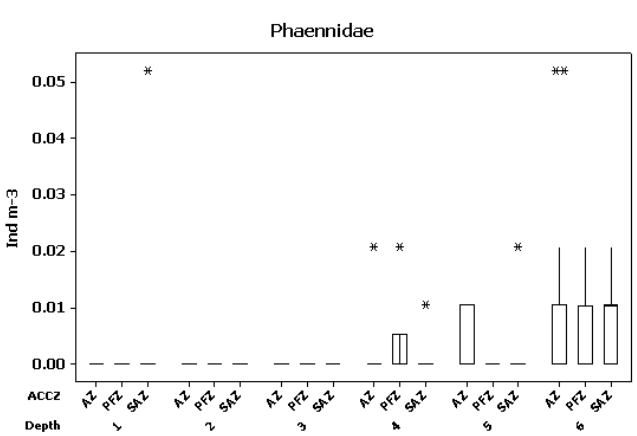

Augaptilidae
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6

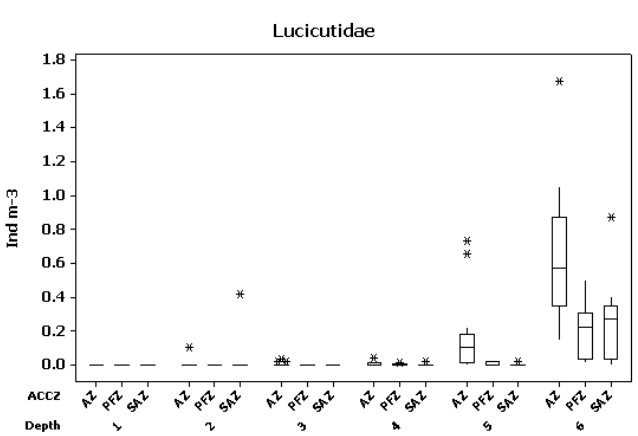

Ostracoda
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6


Oncaeidae
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6


Heterorhabdidae
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6


Spinocalanidae
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6


Phaennidae
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6


Lucicutidae
Ind m-3
ACC2
AZ PFZ SAZ
Depth
1 2 3 4 5 6

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937 Table 1. *Discovery* stations sampled along 80°W by month with respect to ACC Zones.
938 Stations emboldened were originally classified as Antarctic stations by Foxton (1956) and the
939 remainder as sub-Antarctic. Antarctic Circumpolar Current Zones (ACCZ) defined according
940 to potential temperature, salinity and potential density sections and potential temperature-
941 salinity curves (see text). Stations with an asterisk are those where one or more samples are
942 missing or the contents had been spilt.

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	ACCZ		
	Antarctic Zone (AZ)	Polar Frontal Zone (PFZ)	sub-Antarctic Zone (SAZ)
December (1933)	**1220, 1221, 1222, 1223, 1224**	1225, 1226*, 1227*	1228*, 1229
March (1934)	**1312, 1313, 1314, 1315*, 1316**	1317	1318*, 1319, 1320
September (1934)	**1415*, 1416,**	1417, 1418*, 1419*	1420,1421*
October (1934)	**1447**, **1449, 1450**	1446*, 1444*	1441*,1442, 1443,
November (1934)	**1472, 1473, 1474, 1475**	1476	

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949 Table 2: Median plankton abundance (ind. m^{-3} (Q1-Q3)) and biomass (wet mass mg m^{-3}(Q1-
950 Q3)). Biomass derived from settled volume (cm^{-3}) assuming $1cm^3$ =1g wet mass. See
951 original data in Foxton (1956) Table 11c. . The formula π x r^2 x h has been used to estimate
952 abundance and volume per m^{-2} and thence m^{-3}. ACC Zone definitions and abbreviations as
953 Table 1, (n) = no. of samples within each ACC Zone.

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	Depth (m)	AZ (111)	PFZ (50)	SAZ (54)
Abundance	50-0	306 (43-700)	294(194-464)	187 (127-299)
	100-50	294 (177-565)	211 (107-552)	180 (157-239)
	250-100	92 (55-153)	182 (122-195)	93 (66-147)
	500-250	44 (39-72)	54 (35-67)	56 (40-83)
	750-500	20 (13-36)	26 (20-29)	30 (23-46)
	1000-750	13 (8-21)	10 (8-18)	14 (7-24)
Biomass	50-0	21 (5-47)	44 (29-51)	36 (13-60)
	100-50	52 (10-88)	47 (23-153)	36 (23-59)
	250-100	21 (10-40)	42 (16-49)	26 (14-41)
	500-250	19 (12-22)	14 (11-17)	12 (16-23)
	750-500	12 (8-19)	14 (9-17)	14 (11-19)
	1000-750	7 (5-10)	10 (8-13)	9 (7-10)

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963 Table 3: Analysis of Similarities (ANOSIM), testing how well station grouping reflects
964 ACCZ definitions (see text). ACC Zone definition and abbreviations as Table 1. * =
965 significant difference. No. of permutations = 999.

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Data matrix	R statistic	Significance Level (*p*)	Watermass Comparison
0-1000 m			
Differences between ACCZs	0.32	0.008	AZ/PFZ*
	0.87	0.001	AZ/SAZ*
	0.39	0.010	PFZ/SAZ*
500-1000 m (less seasonal migrants)			
Differences between ACCZs	0.25	0.016	AZ/PFZ*
	0.74	0.008	AZ/SAZ*
	0.12	0.130	PFZ/SAZ

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976 Table 4: Abundance (mean ind. m^{-2}, 0-1000 m (±SD)) of the first ten species/taxa in the analysis shown to be contributing
977 most to within group similarity and between group dissimilarity across all 3 groups of stations (no. of stations). Taxa ranked
978 in terms of overall abundance across all groups. ACC Zone definitions and abbreviations as Table 1.
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Species/taxa	AZ(16)	PFZ(5)	SAZ(6)
Oithona similis	22399 (11274)	32167 (15881)	11616 (6456)
Ctenocalanus spp.	8240 (5557)	17167 (15859)	12565 (7039)
Pteropoda	15094 (43509)	359 (753)	62 (128)
Oncaea spp.	10827 (6623)	7742 (6091)	6415 (3691)
Oithona frigida	6300 (2412)	5720 (2774)	4128 (1779)
Microcalanus pygmaeus	3970 (1601)	4587 (820)	7562 (3594)
Calanoid nauplii	3315 (3511)	3480 (3891)	1650 (1075)
Metridia lucens	709 (616)	2598 (2258)	1701 (1165)
Paroithona sp.	31 (39)	858 (815)	4492 (4889)
Rhincalanus gigas	1024 (656)	1784 (499)	864 (952)
Calanus simillimus	740 (2413)	1667(1165)	1664 (1736)
Calanoides acutus	1342 (1051)	610 (1143)	9 (10)
Ctenocalanus/ Clausocalanus copepodites	447 (761)	486(469)	2257 (1949)
Ostracoda	489 (201)	998 (335)	1389 (545)
Chaetognatha spp.	619 (378)	855 (753)	847 (451)
Appendicularians	881 (1803)	236 (266)	533 (1088)
Copepod spp. (Unidentified copepopdites)	742 (828)	332 (256)	774 (399)
Rhincalanus gigas nauplii	783 (1383)	347 (455)	31 (76)
Clausocalanus laticeps	34 (73)	266 (263)	859 (1277)
Subeucalanus longiceps	19 (18)	147 (112)	908 (445)

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Table 5: Mean abundance ind.m^{-2} (±SD) within the depth horizons indicated with respect to ACC Zone grouping (see Table 3). ACC Zone definition and abbreviations as Table 1. (n) number of stations within respective ACC Zones.

Depth	ACC Zone Grouping		
	AZ (16)	PFZ (5)	SAZ (6)
0-1000 m	8.18 x10^4 (5.17 x10^4)	8.50 x10^4(4.40 x10^4)	6.47 x10^4(3.08 x10^4)
	AZ (18)		SAZ /PFZ(15)
500-1000 m	0.80 x10^4 (0.44 x10^4)		0.86 x10^4 (0.44 x10^4)

Table 6: Abundance (mean ind. m^{-2}, 500-1000 m (±SD)) of the first ten species/taxa in the analysis shown to be contributing most to within group similarity and between group dissimilarity across all 3groups of stations (no. of stations). Taxa ranked in terms of overall abundance across all groups. ACC Zone definitions and abbreviations as Table 1.

Species/taxa	AZ (18)	PFZ & SAZ (15)
Oncaea spp.	2989 (2268)	2874 (1501)
Oithona frigida	1983 (963)	1452 (656)
Microcalanus pygmaeus	1238 (1225)	2150 (1831)
Metridia lucens	243 (353)	372 (259)
Metridia curticauda	223 (78)	152 (66)
Calanoid nauplii	194 (151)	170 (84)
Ostracoda spp.	178 (80)	165 (62)
Spinocalanus spp.	225 (215)	72 (43)
Chaetognatha spp.	115 (66)	171 (118)
Lucicutia ovalis	200 (96)	54 (62)
Paroithona sp.	5 (15)	241 (551)
Scolecithriciid copepodites	56 (30)	83 (50)
Pleuromamma robusta	43 (72)	85 (45)
Mormonilla sp.	20 (28)	83 (74)
Siphonophora	12 (13)	51 (53)
Clione antarctica	15 (21)	30 (37)
Paraeuchaeta biloba	8 (14)	22 (13)
Euphausiid nauplii	14 (25)	14 (27)
Thysanöessa spp.	6 (21)	11 (9)
Euaetideus australis	0 (0)	12 (15)

Table 7: Mean (±SD) and median (Q1-Q3) abundance (ind.m^{-2}, per 250 m haul in the 500-1000m depth horizon) of the 20 most abundant species/taxa within the 500-1000 m horizons. Data represent spring (Sept/Oct /Nov) and summer (Dec/March).Only *Spinocalanus* spp. showed a significantly different seasonal abundance (Anova $F_{1, 69}$=5.74, p = 0.019).

Species/taxa	Spring mean (ind. m^{-2}, per 250 m haul in the 500-1000 m depth range)	Summer mean (ind. m^{-2}, per 250 m haul in the 500-1000 m depth range)	Spring median (ind. m^{-2}, per 250 m haul in the 500-1000 m depth range)	Summer median (ind. m^{-2}, per 250 m haul in the 500-1000 m depth range)
Oncaea spp.	1199 (879)	1674 (1381)	915 (585-1681)	1122 (686-2359)
Oithona frigida	835 (835)	850 (454)	717 (364-1065)	727 (587-1086)
Microcalanus pygmaeus	710 (612)	898 (1317)	546 (177-1081)	447 (125-1122)
Metridia lucens	122 (207)	165 (252)	30(8-131)	94 (27-194)
Metridia curticauda	103 (61)	90 (72)	87 (64-126)	83 (23-152)
Calanoid nauplii	89 (87)	86 (77)	83 (42-117)	83 (16-120)
Ostracoda	91(46)	79 (53)	87 (61-110)	73 (35-118)
Spinocalanus spp.	47*(61)	100 (115)	23 (10-62)	73 (31-125)
Chaetognatha	68 (43)	70 (70)	64 (31-89)	42 (25-104)
Lucicutia ovalis	67 (96)	62 (70)	26 (0-102)	34 (3-112)
Paroithona sp.	12 (21)	91 (323)	0 (0-21)	0 (0-31)
Heterorhabdus spp.	36 (25)	39 (32)	32 (18-45)	34 (16-51)
Scolecithriciid copepodites	34 (29)	35 (33)	26 (16-52)	21(10-56)
Pleuromamma robusta	35 (60)	26 (41)	16 (0-45)	5 (0-38)
Mormonilla sp.	28 (39)	23 (35)	10 (0-42)	10 (0-31)
Gaetanus tenuispinus	16 (18)	18 (24)	9 (3-19)	10 (3-27)
Siphonophora	9 (13)	19 (34)	3 (0-12)	8 (0-19)
Pareuchaeta antarctica	14 (13)	9 (14)	10 (5-21)	5 (1-10)
Scaphocalaniid copepodites	9 (13)	13 (15)	5 (2-10)	8 (3-19)
Scolecithricella dentipes	13 (11)	8 (8)	9 (2-23)	8 (3-13)

Table 8: Mean (±SD) number of species/taxa within the 0-1000 m water column with respect to ACC Zone. Of the comparisons carried out among ACC Zones using all taxa and copepods only that between AZ and SAZ was significant; ANOVA $F_{1,\ 20\ df}$ =14.41, p = 0.001 for all taxa and $F_{1,\ 20\ df}$ = 16.58, p=0.001 for copepods alone. ACC Zone definition and abbreviations as Table 1.

Watermass (no. stns)	No. taxonomic categories	No. copepod categories
AZ (17)	60.4 ± 6.1	46.9 ± 3.4
PFZ (4)	61.5 ± 6.2	47.3 ± 4.7
SAZ (6)	73.7 ± 9.6	57.0 ± 8.5

Table 9. Number of species of copepods identified within each ACC Zone with respect to Order and Family. Family (n) = no. of species identified within family across all groupings. ACC Zone definition and abbreviations as Table 1. ACCZ (n) = no. samples analysed.

		AZ (117)	PFZ 44)	SAZ (54)
Order	Family			
Calanoida				
	Calanidae (4)	4	3	4
	Eucalanidae(5)	2	4	4
	Spinocalanidae(2)	2	1	1
	Clausocalanidae (4)	4	4	4
	Tharybidae (1)	1	1	1
	Stephidae (1)	1	0	0
	Aetideidae (16)	8	8	15
	Euchaetidae (7)	5	4	6
	Phaennidae (5)	3	4	3
	Scolecitrichidae (13)	11	8	8
	Arietellidae (1)	1	0	1
	Augaptilidae (11)	4	5	9
	Heterorhabdidae (6)	4	3	6
	Lucicutiidae (6)	6	2	3
	Metridinidae (6)	5	6	5
	Phyllopodidae (1)	1	1	1
	Candaciidae (1)	1	1	1
	Bathypontidae (1)	1	1	1
Mormonilloida				
	Mormonillidae (1)	1	1	1
Cyclopoida				
	Oithoniidae (4)	4	3	4
Harpacticoida				
	Ectinosomatidae (1)	1	1	1
	Aegisthidae (1)	0	0	1
Poecilostomatoida				
	Oncaeidae (2)	2	2	2
Siphonostomatoida				
	Ratanidae (1)	0	0	1
	Totals	72	63	83

Highlights

1. Plankton samples from 1930's *Discovery Investigations* in the Southern Ocean analysed

2. Depth was the strongest factor separating samples

3. Mean zooplankton abundance in the epipelagic was ~ 25 times greater than at 1000 m

4. Seasonal signals across all data became less distinct with depth.

5. Rarefaction analysis revealed that depth was a major influence on diversity.